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# **The control and prediction of the voluntary food intake of pigs fed poor quality foods**

**Emma Christine Whittemore**

A thesis submitted towards the degree of *Doctor of Philosophy* at the  
University of Edinburgh.

March 2002



## Dedication

This work is dedicated to my family who have been a constant source of love, support, encouragement and inspiration to me. Thank You.

*“It was the best of times, it was the worst of times”*

Charles Dickens, A Tale of Two Cities.

## Abstract

The purpose of this thesis was to investigate, in a series of four experiments, the factors that are important for the control and prediction of the voluntary food intake of growing pigs fed poor quality foods.

The aim of Experiments 1 and 2 was to provide a severe test of two current conceptual frameworks available for the understanding and prediction of food intake. Framework 1 assumes that intake will be that which allows genetic performance to be achieved. If this is not achieved then it is assumed to be because there is a constraint to food intake (e.g. the bulk content of the food) operating. Framework 2 sees intake as being a consequence of a process of optimisation, such that biological efficiency (rate of net energy ingested per litre of oxygen consumed) is maximised. The experiments tested areas where the frameworks differed in their predictions of intake on poor quality foods. Experiment 1 tested the effect of ambient temperature on the intake of foods of differing bulk content, Experiment 2 tested the effect of a period of reduced growth on the subsequent intake of foods of differing bulk content. The results of both experiments were in closer agreement with the predictions of Framework 1. It was concluded that the results provided no evidence that the idea that intake on poor quality foods in young growing pigs is constrained by gut capacity should be rejected.

Experiment 3 investigated the effect of giving foods of differing bulk content on the short term feeding behaviour (STFB) of growing pigs. It was expected that differences in bulk content between the foods would result in different levels of intake that would be reflected as differences in STFB. Three hypotheses were developed based on ideas about the way in which a physical constraint to intake might operate. H1; there would be less diurnal variation in feeding on high bulk foods that limit intake. H2; feeding patterns on bulky foods would be less flexible than those on a control food when feeding time is limited by reducing time of access to the feeder. H3; when the composition of the food offered is changed intake and hence STFB will be rapidly altered to suit the new food. The results of the experiment were in agreement with H2 and H3. Pigs fed higher bulk foods did not maintain intake or performance when time of access to the feeder was reduced, this was mainly due to the absence of any adaptive change in STFB. In agreement with H3, when the composition of the food offered was changed there was a rapid change in STFB so that it became appropriate to the new food. These results are in agreement with the idea that intake on bulky foods is physically constrained. Contrary to expectation, a higher bulk content had no significant effect on the diurnal intake pattern of pigs given 24 hours access to food, the reason for this remains unclear.

The final experiment investigated the effect of degree of maturity on the capacity to consume food bulk. This was done by feeding a constraining food (a food high in bulk that was intended to limit the growth of the pigs to which it was fed) at one of three different degrees of maturity (12, 36 or 108kg). The aim of this final experiment was to determine how capacity for bulk (bulk units/ kg day) changed with increasing maturity and to determine if the hypothesis that the capacity to consume food bulk is proportional to liveweight can be extended for use in pigs greater than 45kg. The idea that constrained food intake is proportional to liveweight did not hold for pigs that were greater than 40kg, as the scaled capacity for bulk was not constant but decreased with an increase in liveweight beyond 40 kg. The relationship between liveweight ( $W$ , kg) and the absolute capacity for



bulk (Cap, kg water holding capacity/day) was accurately described by the quadratic function  $Cap = (0.230.W) - (0.000476.W^2)$ .

A change in food type to one with a higher bulk content may have important consequences for both intake and performance. Initially intake and performance will be reduced. Over time, as the animal becomes adapted to the new food, intake will increase until an equilibrium intake appropriate to that food is reached. Current models that predict intake over time assume that the animal is always fully adapted to the food that it is on. A model was developed with the aim of predicting intake and performance during the adaptation period to a new food. The model is based upon the assumption that that an animal has a desired rate of intake (DFI) which is determined by the requirements for protein and lipid deposition and maintenance. DFI may not be met if a bulk constraint to intake exists. Where a bulk constraint operates intake is calculated as the constrained intake (CFI) which is a function of the animals capacity to consume food bulk and the bulk content of the food. The time taken to adapt to a new food is assumed to depend on the difference in bulk content between the first and second food. The initial capacity to consume food bulk is related to the bulk content of the current food. Thereafter, capacity will increase over time to a maximum. The rate at which capacity is increased is assumed to be the same for all pigs regardless of the type of food being fed, and the increase in capacity over time is assumed to be linear. The magnitude and direction of response of the model is in close agreement with relevant observed data, the underlying theoretical assumptions of the model are concluded to be reasonable.

Taken together the results of the work completed in this thesis show that the idea that food intake on high bulk foods is constrained by the capacity of the gastrointestinal tract in relation to the bulk content of the food can account for observed food intakes on high bulk foods. Physical constraints to food intake are thus concluded to be important for the control and prediction of food intake on poor quality (high bulk) foods. Food intake prediction models that are based on this assumption will therefore have a good theoretical basis and should provide an accurate description of change in intake over time.

## Declaration

I, hereby declare that this thesis is of my own composition, and that all assistance from other people has been duly acknowledged. The results presented herein have not previously been admitted for any other degree or qualification.

Emma Christine Whittemore

March 2002

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Firstly, and most importantly I would like to thank my supervisors Professor Ilias Kyriazakis and Mr Gerry Emmans. It has been both a great privilege and a pleasure, it is not often that you get the opportunity to work with not one but two such exceptional scientists, even if their reputation does precede them! They have been a constant source of support, advice, encouragement, inspiration, and patience. Their supervision has been outstanding and their role in my scientific development over the past three years invaluable. I want to thank them for devoting so much of their time and energy to my supervision and for teaching me about good, imaginative and interesting science. Special thanks must also go to Dr. Bert Tolkamp for his help, encouragement and advice with the first three Chapters of the thesis. His kind nature and willingness to help at all times is greatly appreciated.

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This work enjoyed generous support, including my studentship from three industrial sponsors - PIC (now Sygen), Finnfeeds, and Dalgety Feeds (now ABN). I would like to acknowledge the intellectual and moral support over the past three years from my contacts Pieter Knap of Sygen, Steve Jagger of ABN and Howard Simmins of Finnfeeds. In particular I would like to thank Pieter for the supply of Hopjes. I would also like to acknowledge the financial support of SEERAD for the experimental part of the project.

Thanks must also go to all the friends, fellow students and ABD staff that I have met during my studies. In particular to all in the Animal Nutrition and Health Department, your ability to criticise is second to none! Special thanks must go to Hannah Bornett, for her support, advice, and friendship during the first two years of my PhD. Our lunchtime walks kept me sane. Thanks also to all the other fellow postgrads who have helped to make the postgraduate room a pleasant environment within which to work. Thanks must also go to Jos for letting me invade his office on numerous occasions without once complaining.

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# **CHAPTER 1**

## **Introduction**

## **1.1 THE PROBLEM OF FOOD INTAKE PREDICTION IN PIGS**

The ability to accurately predict food intake under a range of relevant circumstances will improve response prediction, allow financial and management decisions to be improved, and diet formulation and feeding strategies to be optimised. Although the potential benefits of accurate food intake prediction are clear, few attempts to do this have been effective in pigs.

The lack of good general methods for predicting food intake may, in part, be attributed to the past use of restricted feeding regimes for pigs (Kyriazakis and Emmans, 1999), which led to early models of pig growth treating food intake as an input (e.g. Whittemore and Fawcett, 1974). Pomar *et al.* (1991) and de Lange (1995) have also adopted this approach. However, the use of *ad libitum* feeding means that food intake has to be treated, not as an input but rather, as a variable to be predicted.

Most of the current models in use seek to quantify food intake for the practical purpose of defining nutrient requirement (e.g. ARC 1981 and NRC 1987), but are inadequate in their function. The common method of empirically relating food intake to a single variable, most often liveweight (e.g. ARC, 1981; Whittemore 1983; NRC, 1987), is inadequate because it fails to account for the effects of environment or genotype on food intake and fails also to adequately account for the effects of food quality. Methods of food intake prediction based solely on animal or food characteristics cannot be seen to have generality and are therefore bound to fail (Mertens, 1994; Kyriazakis and Emmans, 1999).

The quantitative determination of actual food intake is necessarily complex due to the nature of the interactions that affect food intake. It was concluded in recent reviews by Black (2000) and Whittemore *et al.* (2001) that currently there is no accurate means of predicting food intake. The quantitative determination of food intake is however, vital if daily pig nutrition is to be optimised.



## **1.2 THEORIES OF FOOD INTAKE**

### **1.2.1 DESIRED FOOD INTAKE**

An alternative approach for the prediction of food intake in immature farm animals was proposed by Emmans (1981). The approach assumes that the pig eats to attain its genetic potential. It is assumed that genetic potential will determine the rate at which a given food will be consumed. Thus, an animal will have a desired food intake (DFI) that it will aim to achieve. According to this system, desired food intake and hence genetic potential may not be achieved due to constraints arising from the food being fed or due to constraints arising from the environment. Black *et al.* (1986), Ferguson *et al.* (1994), Poppi *et al.* (1994), Whittemore *et al.* (1995), Emmans (1997) and Kyriazakis and Emmans (1999) have advocated this approach.

The focus of this thesis, and one of the most relevant constraints in modern pig production, is that of the bulk content of the food. Where a bulk constraint operates actual food intake is predicted to be less than desired food intake and is calculated as constrained food intake (CFI) (e.g. Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998; Kyriazakis and Emmans, 1999). CFI is considered to be a function of the bulk content of the food and the animal's capacity for food bulk.

### **1.2.2 AN ALTERNATIVE THEORY OF FOOD INTAKE**

In recent years the idea that animals aim to meet requirements subject to constraints has been strongly criticised for its failure to account for observed variation in food intake in ruminants on foods of moderate and poor quality (Grovm, 1987; Ketelaars and Tolkamp, 1992; Tolkamp 1999). Tolkamp and Ketelaars (1992) presented an alternative theory for the control of food intake. This theory considers food intake to be the result of some process of biological optimisation such that maximum efficiency is achieved. Efficiency here is the ratio of net energy intake per unit of oxygen consumed. An animal is predicted to eat at the optimum level, which is that

which allows the amount of net energy consumed per litre of oxygen consumed to be maximised. Foods of different quality, with different bulk contents, will have different optimum levels at which this is achieved.

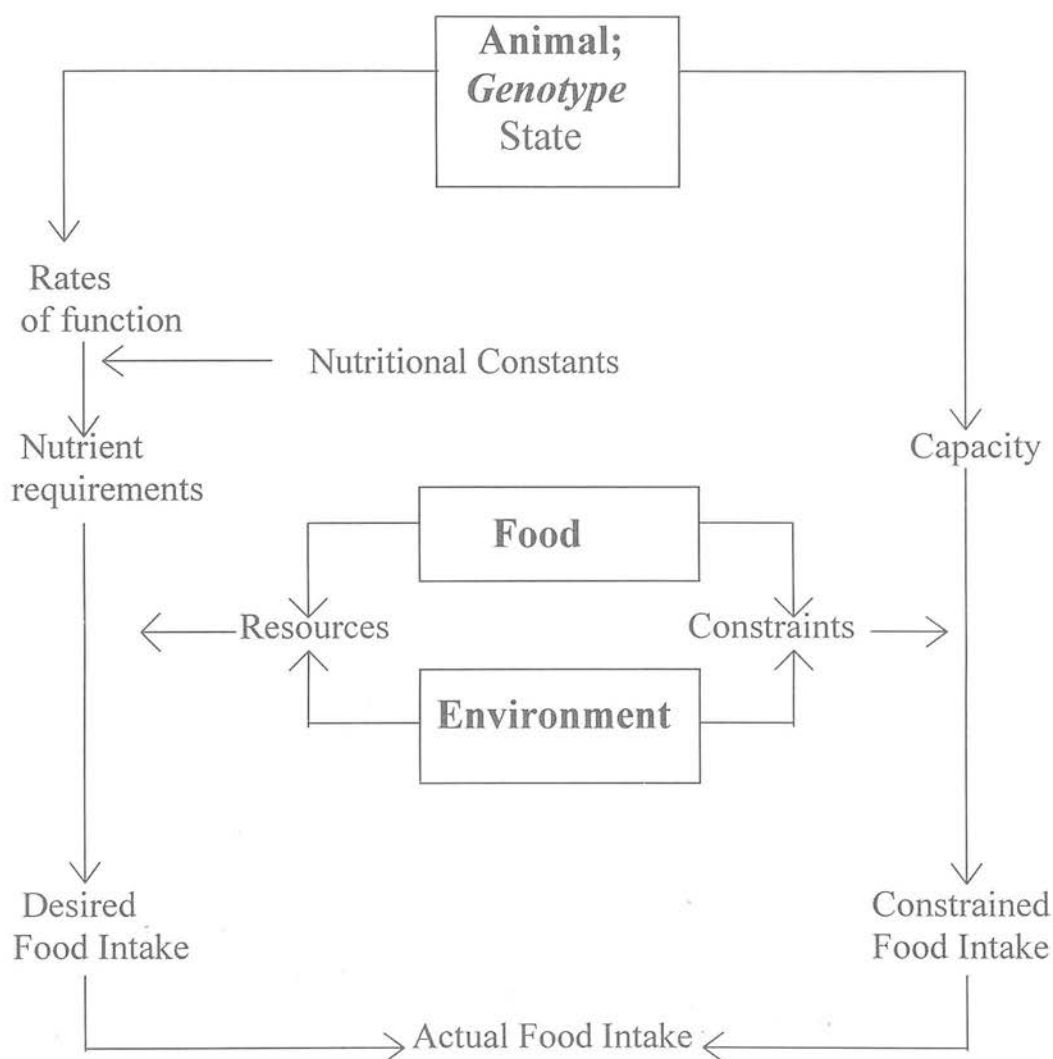
### 1.2.3 INTEGRATIVE THEORIES OF FOOD INTAKE

There is a view that food intake is the result of the animal integrating a large number of physiological signals (e.g Poppi *et al.*, 1994; Forbes, 1995; Berthoud, 2000). Such an approach to food intake prediction requires knowledge of the underlying physiological controls of food intake. Whilst there is a huge literature on the possible physiological mechanisms underlying the control of food intake (e.g. Bernadis and Bellinger, 1993; Feifel and Vaccarino, 1994; Forbes, 1995), there is no evidence to suggest that such an approach can be useful for the prediction of food intake (Kyriazakis and Emmans, 1999; Emmans and Kyriazakis 2001). The past failure of this approach was also recognised by Berthoud (2000) '*Almost a century of intense research has been unable to identify clearly the neural substrate subserving these behavioural functions.*' Thus, as this theory of food intake control seems to have no prospect of contributing to accurate food intake prediction it will not be considered any further in this thesis.

The aim of the remainder of this chapter is to review the existing literature that provides a background to the control and prediction of food intake of pigs on poor quality (high bulk) foods. This chapter will focus mainly on the development and discussion of the maximum performance subject to constraints theory and the maximum efficiency theory described above, which are seen as the two main theories currently available for the prediction and understanding of the control of food intake on bulky foods.

### 1.3 FRAMEWORK 1 - MAXIMISATION OF PERFORMANCE

#### SUBJECT TO CONSTRAINTS



**Figure 1.2.** A schematic representation of the theory that animals eat meet their requirements subject to constraints (taken from Emmans and Oldham, 1988).

The basis of an accurate food intake prediction model is a general, quantified theory of food intake. Most current food intake prediction models are based upon the implicit assumption that an animal will eat at a level that allows genetic performance

to be achieved unless food intake is constrained in some way. Figure 1.2 illustrates the theory of animals eating to meet requirements subject to constraints. The starting point is the description of the animal in terms of its genotype and its current state. From this potential performance can be predicted in terms of rates and from these potential rates the requirement for food resources can then be calculated using a set of constants (Emmans and Kyriazakis, 2001). Importantly, therefore, food intake is an output of, not an input to, the system.

### 1.3.1 PREDICTION OF FOOD INTAKE IN THE ABSENCE OF CONSTRAINTS

In this section the framework that is to be used in this thesis is described. It is assumed that an animal will have a potential rate of 'normal' growth and composition, and that it will seek to eat at a level that will allow this to be achieved. In a thermally neutral environment where all nutrient to energy ratios are adequate the desired food intake (DFI) is, therefore, the rate of food intake required to meet the current requirements for energy. The requirement for energy is determined by the potential for protein deposition, (dP/dt, kg/day) the desired rate of lipid growth (dL/dt, kg/day) and the requirement for maintenance (Kyriazakis and Emmans, 1999). Where energy is not the first limiting resource, DFI will be that needed to meet the requirement for the first limiting nutrient.

In the absence of constraints an animal is, therefore, presumed to eat at a level that will allow its requirements to be met. Where energy is the first limiting resource, DFI is then calculated as

$$DFI = RQ/FEC \quad \text{kg/day}$$

where RQ is the requirement for energy (MJ/day) and FEC is the food energy content (MJ/kg). As long as RQ can be predicted, and FEC is known or can be calculated, then DFI can be predicted. Under non-limiting conditions, the requirement for energy by the growing animal is the sum of the requirements for maintenance, protein retention and lipid retention as follows

$$RQ = E_m + E_{\text{gain}} \quad \text{MJ/day}$$

where  $E_m$  is the energy needed for maintenance (MJ/day), and  $E_{\text{gain}}$  (MJ/day) is the energy required for potential protein and lipid growth at a given weight.

The energy required for maintenance can be made a function of the current and mature protein weights,  $P$  and  $P_m$  (Emmans and Fisher, 1986) so that

$$E_m = M_e \cdot P / (P_m^{0.27}) \quad (\text{MJ/day})$$

where  $M_e$  is a constant the value of which is uncorrelated with mature protein weight.

The amount of energy required for gain ( $E_{\text{gain}}$ , MJ/day) is calculated as

$$E_{\text{gain}} = y_1 \cdot dP/dt + y_2 \cdot dL/dt \quad (\text{MJ/day})$$

where  $dP/dt$  and  $dL/dt$  are the rates of protein and lipid deposition respectively (kg/day) and  $y_1$  and  $y_2$  are the constants representing the amount of energy required for a unit of protein and lipid to be retained (MJ/kg). The estimation of protein and lipid retention requires the estimation of mature protein weight, fatness at maturity and the Gompertz growth parameter, as well as the estimation of current protein weight (Emmans and Fisher, 1986; Emmans, 1988; Emmans and Kyriazakis, 1997). It is assumed that potential protein growth is a Gompertz function so that

$$dP/dt = B \cdot P \cdot \log_e(P_m/P) \quad (\text{kg/day})$$

where  $P$  is the current protein weight (kg),  $P_m$  is mature protein weight (kg) and  $B$  is the Gompertz growth parameter. It is also assumed that lipid growth is a Gompertz function so that

$$dL/dt = B.L.\log_e(L_m/L) \quad (\text{kg/day})$$

The assumption that B has the same value for protein and lipid has the consequence that under non-limiting conditions the weight of lipid can be expressed as an allometric function of the current protein weight (Emmans, 1988; Emmans and Kyriazakis, 1997), so that

$$L = x. P^b \quad (\text{kg})$$

### **1.3.2 FOOD INTAKE IN THE PRESENCE OF CONSTRAINTS**

It is possible that desired food intake might not be achieved due to constraints arising from the food or the environment. The presence of a constraint will result in actual food intake being less than DFI and hence performance will be reduced. Constraints include the bulk content of the food, which may limit food intake, the environmental temperature, which will affect the pig's ability to lose heat, or the presence of toxins in the food (Kyriazakis and Emmans, 1999).

#### ***1.3.2.1 EFFECT OF TEMPERATURE ON FOOD INTAKE***

Environmental conditions are known to have considerable effects on voluntary food intake. It is important to quantify the effect of temperature on food intake, if food intake and hence growth rate are to be predicted accurately. Environmental temperature influences food intake through its effect on a pig's ability to lose heat. At ambient temperatures below the lower critical temperature there will an increased loss of heat to the environment and so heat production must then be increased if body temperature is to be maintained. Under these conditions food intake is predicted to be increased. If food intake is not able to be increased by an amount sufficient to compensate for the increased heat loss then growth rate will be reduced (Neinaber *et al.*, 1990). Under these circumstances the additional energy required to maintain body temperature may come at the expense of fat deposition. On the other hand, at

ambient temperatures above the upper critical temperature the ability to lose heat will be limited so that the amount of heat lost to the environment will be less than the amount of heat produced by normal metabolism. Here intake is predicted to be reduced, in an attempt to reduce heat production, until possible heat loss and actual heat production are equal (Black *et al.*, 1999). As intake is reduced liveweight gain will become less. The rate of fat deposition may decline more than the rate of protein deposition so that the pig becomes leaner.

Work by Black *et al.* (1986), Ferguson *et al.* (1994) and Poppi *et al.*, (1994) has produced equations for predicting heat loss. Black *et al.* (1986) simulated energy and amino acid utilisation from birth to maturity in pigs. Here, potential performance was assumed to be affected by interactions between food composition, genotype, reproductive performance, environmental conditions and physiological status. Ferguson *et al.*, (1994) predicted constrained food intake by considering the potential growth rate, nutrient requirements, nutrient supply and the environment simultaneously. The idea that food intake will be that determined by the first of several limiting constraints was adopted by Poppi *et al.* (1994). They identified six metabolic and physical factors that limited intake: rate of intake, faecal output, rumen fill, genetic potential for protein deposition, heat dissipation and ATP degradation. The maximum intake able to be achieved on each of these pathways was then calculated. Predicted intake was taken to be the lowest intake produced by any pathway. One of the problems with the approach adopted by Poppi *et al.* (1994) was that for some diets more than one limiting pathway was identified. This may lead to the incorrect rejection of a hypothesis when its removal during experimentation does not lead to the expected increase in food intake.

#### 1.3.2.2 EFFECT OF BULK ON FOOD INTAKE

Traditionally pigs have been fed diets based on a high content of cereals and high-value protein supplements. Although currently the use of high bulk foods is not common place in Western pig production, direct competition with humans for cereals may lead to a situation where alternative foodstuffs for pigs need to be sought.

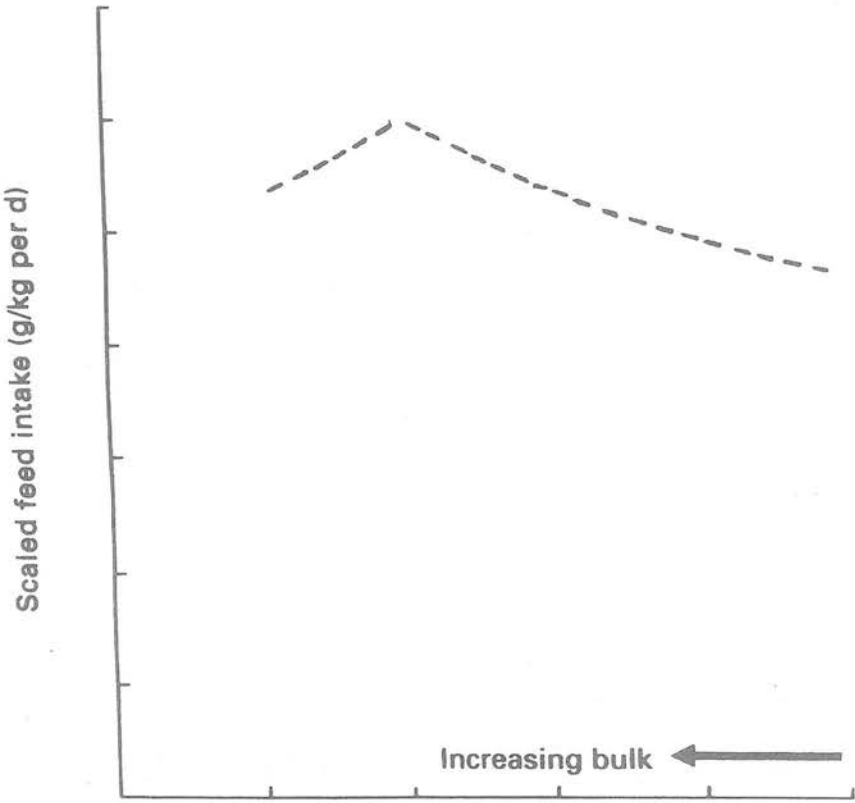
Fibrous materials are already used for pigs in China and Western Australia. The feeding of high bulk foods has been shown to have a number of nutritional, health and welfare benefits, particularly for pregnant and dry sows, such as a reduction in stereotyped and aggressive behaviours, and reduced hunger and frustration (for reviews see Low 1985; Lee and Close, 1987; Meunier-Salaun *et al.*, 2001). The use of fibrous materials and their by-products as an alternative foodstuff for pigs continues, therefore, to receive considerable attention. As most current methods of food intake prediction fail to adequately account for the effects of food bulk on food intake there exists the need for an effective method for predicting the food intake of pigs fed high bulk foods.

When a highly digestible food is progressively diluted by a less digestible food with a higher content of bulk, the rate of food intake will initially increase in such a way that energy intake remains roughly constant and performance is maintained. However, the extent to which a pig can increase food intake as the bulk content of the diet increases is limited. Beyond a critical point (Figure 1.1), food and energy intake will fall and performance will be reduced as dilution progresses further (e.g. Owen and Ridgman, 1968; Cole *et al.*, 1968; Kennelly and Aherne, 1980; Cole and Chadd, 1989; Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998, for growing pigs, Brouns *et al.*, 1995; Vestergaard and Danielsen, 1998, for pregnant sows). According to the idea that a pig eats to attain a desired food intake subject only to the presence of constraints, this critical point reflects the physical capacity of the animal for bulk. (Emmans and Fisher, 1986; Cole and Chadd, 1989).

Initially a change to a food of much higher bulk content causes a reduction in food intake (e.g. Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). Over time, however, intake is gradually increased, as the animal becomes adapted to the new food. When the upper limit to consume food bulk has been reached the amount of food eaten at that bodyweight will not be able to be increased further. At this point the animal is said to be adapted to the food that it is on and is considered to have reached an adapted or 'equilibrium' level of intake appropriate to that food (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). This equilibrium level of intake reflects the



maximum capacity for the food being consumed. It is the equilibrium intake that must first, be used to develop predictive equations. It is also, important to know how long it will take an animal to become adapted to a new food if better predictive equations are to be developed.



*Figure 1.1 The effect of progressively diluting a highly digestible food with a less digestible food of a higher bulk content on food intake. Taken from Kyriazakis and Emmans, 1995.*

Adaptation is a direct reflection of changes in the gastrointestinal tract as it accommodates to the digestion of high bulk foods, and to an increase in gut fill. The feeding of high bulk foods has been shown to cause an increase in empty gastrointestinal weight and gut length (Hansen *et al.*, 1992; Kyriazakis and Emmans, 1995; Pluske *et al.*, 1998). The digestion of high bulk foods occurs mainly in the large intestine as a result of their high non starch polysaccharide content and it is this area of the gut that is most affected by their consumption (Hansen *et al.*, 1992; Kyriazakis and Emmans, 1995; Pluske *et al.*, 1998). The length of time taken to adapt to a bulky food is affected by the bulk content of the food being fed and also by previous nutritional history. Previous experience of a bulky food reduces the time taken to adapt to, and increases the intake of, bulky foods (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). In young growing pigs (12 – 40 kg) adaptation is thought to take between 7 and 14 days (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). The length of time required for adaptation in pigs greater than about 40kg is not known, although it might be expected that as the pig grows the gastrointestinal tract will become less flexible and hence the time taken for adaptation will be increased. Adaptation in older pigs requires further investigation if predictive equations that are relevant across the whole growing period are to be developed.

Food intake on bulky foods is a function of the animal's capacity for food bulk and the bulk content of the food. In young growing pigs the maximum capacity to consume food bulk has been shown to be roughly proportional to liveweight (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). There is, however, a lack of appropriate methods for determining the bulk content of a food. Traditional methods such as those aimed at measuring the indigestibility of a food (e.g. crude fibre, CF, neutral detergent fibre, NDF and acid detergent fibre, ADF) have been shown to be inadequate in accounting for the effects of bulk on food intake (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). For example, food intake is depressed more on foods based on highly digestible materials such as sugar beet pulp than on foods based on less digestible materials such as wheatbran (Brouns *et al.*, 1991). In the work of Kyriazakis and Emmans (1995) measurements of digestibility, density, crude fibre, and NDF could not account for the effects of food bulk on food intake.

The work of Kyriazakis and Emmans (1995) and Tsaras *et al.* (1998) found water-holding capacity (WHC) to be an appropriate indicator of the bulk content of a food. It was able to account satisfactorily for the effects of bulk upon the food intake of growing pigs. A food's WHC is its ability to hold water within its matrix. The more water a food can trap and hold within its matrix the more it will swell, and hence the more space it will occupy. Intake was found to be directly proportional to the reciprocal of the WHC value of a food (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998).

### 1.3.2.3 PREDICTING FOOD INTAKE ON BULKY FOODS

In the past, constrained food intake (CFI) on a bulky food has been made a direct function of liveweight. Black *et al.* (1986) proposed that constrained food intake could be estimated from liveweight, W,

$$\text{CFI} = 0.111W^{0.80} \quad (\text{kg/day})$$

As no attempt was made to account for differences in food composition this equation must fail to have a general application across a range of different foods (Tsaras *et al.*, 1998). More recently Whittemore (1998), following the work of Fergusson *et al.* (1994) also related constrained food intake directly to liveweight

$$\text{CFI} = 0.0013W/(1 - \text{digestibility coefficient}) \quad (\text{kg/day})$$

The inclusion of a digestibility coefficient makes some attempt to account for differences in food composition. However, the use of digestibility as a measure of bulk content is not likely to be general (Brouns *et al.*, 1991; Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998).

A food's WHC was found to be a good indicator of food intake over a wide range of bulky materials (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). Therefore, if

constrained food intake (CFI) is a function of the capacity to consume food bulk and the bulk content of the food, CFI can be given by

$$CFI = C_{whc}/WHC \quad (\text{kg/day})$$

where  $C_{whc}$  (units/day) is the maximum capacity for water holding capacity and WHC (units/kg dry food) is the water holding capacity of the food. For young growing pigs in the weight range of between 12 and 40 kg Kyriazakis and Emmans (1995) and Tsaras *et al.* (1998) showed that the maximum capacity to consume food bulk at any point in time was directly proportional to liveweight so that

$$C_{whc} = z \cdot W \quad (\text{units/day})$$

This methodology for the prediction of constrained food intake has been tested only over the limited weight range of 12 – 40 kg. There is no *a priori* reason to assume that it will hold for pigs that are greater than 40 kg in liveweight. Investigation on heavier pigs is needed if the methodology is to be extended.

Kyriazakis and Emmans (1995) suggested a value of  $z = 0.17$  (units/day), while Tsaras *et al.* (1998) suggested a value of  $z = 0.23$  (units/day). The difference is large and may be related to differences in the methodology used to measure WHC. The WHC values of apparently similar diets were higher in the work of Tsaras *et al.* (1998) than in the work of Kyriazakis and Emmans (1995). In the method of Kyriazakis and Emmans (1995) the food samples were oven dried before WHC was calculated, in the work of Tsaras *et al.* (1998) the food samples were freeze dried. WHC is more a function of fibre structure than chemical composition (Robertson and Eastwood, 1981). The method of drying is known to affect fibre structure, which in turn can affect the WHC of a material (Robertson and Eastwood, 1981; Tsaras *et al.*, 1998). The differences in WHC and hence the difference in the values of  $z$  between the work of Kyriazakis and Emmans (1995) and Tsaras *et al.* (1998) could be accounted for by the differences in WHC methodology. It is thus important that the

methodology for calculating WHC values is standardised, as  $z$  apparently varies with the methodology used.

### 1.3.3 CRITIQUE OF FRAMEWORK I

The ideas that animals aim to eat at a level that will allow genetic potential to be achieved unless food intake is constrained and that food intake on high bulk foods is limited by physical capacity are now generally accepted in animal science. These concepts form the basis of most work aimed at explaining variation in food intake on poor quality foods. In fact the use of the idea that food intake on high bulk foods is physically constrained has become so universal that Tolkamp (1999) states that *'all theories of food intake in ruminants rely on the idea that at least part of the variation in forage intake in ruminants can be related to physical constraints'*. While Grovum (1987) concludes that the theory has become so *'well entrenched'* that it has *'developed into dogma'*. However, in recent years the idea that animals aim to maximise performance subject to constraints has been criticised particularly in its application to ruminants (Grovum, 1987; Ketelaars and Tolkamp, 1992; Tolkamp, 1999; Pittroff and Kothmann, 1999; Poppi *et al.*, 2000). Although most of the criticisms stem from observations made in ruminants (comparable work in monogastrics is not available), a framework must be general and any criticism must be seen to be a general criticism of the framework.

#### *1.3.3.1 THE EXPERIMENTAL EVIDENCE*

The idea that food intake is constrained by an animals capacity to consume food bulk does not adequately account for the observed food intake of ruminant animals fed foods of moderate and poor quality. Ruminants show an enormous flexibility in their ability to consume forages. Depending on their physiological state they are able to adapt intake and change total rumen fill apparently regardless of the type of food

being fed (e.g. Johnson and Combs, 1991; 1992). This ability to increase rumen fill can be extensive; Mowat (1963, cited in Grovum, 1987) reported increases in total fill (digesta load and bladder) of up to 68% in the reticulorumen after the addition of water-filled bladders to the rumen. In ruminants fed forages (both mixed with concentrate and fed alone) large increases in food intake and rumen fill in response to changes in physiological state such as pregnancy and lactation are common (e.g. Weston, 1982; Weston, 1988; Stanley *et al.*, 1992; Kaske and Groth, 1997). Reductions in food intake during pregnancy when they are evident are often less than that expected based on the decrease in ruminal capacity as a result of increased foetal mass (Stanley *et al.*, 1992). Such observations are not in agreement with the idea of a physical regulation to food intake where physical fill is expected to be constant. The idea that animals aim to maximise performance subject to constraints implies that the ability to consume food bulk should be little affected by physiological state. Evidence that the ability to consume bulk is a function of physiological state does not fit easily into this concept.

The effects of adding inert materials directly to the rumen are frequently taken as being the most direct evidence in favour of the idea that food intake is limited by an animal's capacity to consume food bulk in relation to gut capacity. A number of experiments have shown that addition of inert materials, which are intended to occupy space but not to have any other effects on rumen stability and function, causes a reduction in food intake (e.g. Balch and Campling, 1962; Welch, 1967). This has been interpreted to be evidence that the size of the gastrointestinal tract physically limits food intake. The rumen is a complex organ consisting of many ridges, pouches, pillars and grooves in which the digesta is moved around and contractions of the rumen wall result in a complicated multidirectional movement of the digesta (Tolkamp, 1999). It is conceivable, therefore, that the addition of large amounts of 'inert' material will disturb the normal functioning of this complex organ. Indeed, more recent work looking at the addition of 'inert' materials to the rumen has shown that the addition of such materials has profound effects on rumen function, affecting pH, time spent ruminating, frequency of contractions and the acetate:propionate ratio (e.g. Baumont *et al.*, 1990; Johnson and Combs, 1991). Any

effect on rumen functioning would be expected to have some influence on food intake (e.g. Egan, 1966; Weston, 1966; Williams *et al.*, 1985). If this is the case then changes in food intake that have been attributed to physical limitation may actually have been the result of disturbances to normal rumen function.

Although, some similar work has been completed in monogastric species where inert materials such as air or water filled balloons have been added to the stomach, the results are ambiguous. Work done by Lepionka *et al.* (1997) in pigs, found that the addition of an air filled balloon occupying about 50% of the stomach volume had no effect on food intake. However, it is worth noting that the pigs were only fed a test meal of 500g. In rats, the addition of balloons representing about one third of the stomach volume caused a significant reduction in food intake in the short term (Geliebter *et al.* 1987), but in man a 400ml balloon occupying about 25% of the stomach volume failed to have any significant effects on food intake (Geliebter *et al.*, 1990). Share *et al.* (1952) showed the addition of water filled balloons to the stomach of dogs caused a persistent reduction in food intake, the degree of the reduction being correlated with the amount of space the balloon occupied. In most of these cases however, the test diet was not of a bulky nature, so that the lack of any reduction in food intake is therefore not surprising.

The stomach of monogastrics cannot be seen to be equivalent to the rumen. When comparing the two species, the effect of bulk on the large intestine would seem to be of more relevance than the effect of inert materials on the stomach. In pigs the large intestine is the site of microbial digestion of bulky foods that contain a high level of fibrous material. The addition of bulky materials to the diets of pigs has been shown to cause a reduction in food intake that is generally attributed to a physical limitation. However, the feeding of high bulk foods has also been shown to affect the ratio of butyric acid produced relative to other short chain fatty acids (Bach Knudsen *et al.*, 1990; 1993), to reduce the pH in the large intestine, and to increase the viscosity of the intestinal contents (Bach Knudsen *et al.*, 1990). Luminal pH may be important for the growth and metabolism of colonic epithelial cells (Lupton *et al.*, 1988), while increased viscosity affects rate of passage and the extent of digestion of food

macromolecules (Moughan *et al.*, 1999). Such evidence suggests that the addition of bulky material may affect the functioning of the large intestine. If this is the case then it may be difficult to ascertain with any certainty that reductions in food intake on high bulk foods are due to a physical limitation to food intake and not as a result of altered colonic/caecal function.

#### *1.3.3.2 CRITICISMS OF CONRAD, PRATT AND HIBBS (1964)*

The model of Conrad *et al.* (1964) has been particularly influential in the development of the maximum performance subject to constraints theory. This work on cattle concluded that, on foods with a dry matter digestibility of less than 67%, the volume of the gastrointestinal tract limited intake. Work done by Adolph (1947) and Smith *et al.* (1962) in rats and Mraz *et al.* (1956) in chickens had found that the dilution of diets with bulky materials had a negative effect on food intake and performance. The paper of Conrad *et al.* (1964) was, however, one of the first to conclude that physical factors were of prime importance for the control of food intake on high bulk foods, and that the relative importance of physiological and physical factors regulating food intake changed with decreasing digestibility. It is considered to provide evidence in favour of the presence of a physical constraint because it showed that food intake on bulky foods could be predicted well from factors that describe physical limits to intake such as liveweight, faecal output and digestibility and it is still frequently and favourably cited. It has influenced the main framework used here (Figure 1.2)

The work of Conrad *et al.* (1964) has however, been heavily criticised by Grovum (1987) Ketelaars and Tolkamp (1992) and Tolkamp (1999). This work does not see the paper of Conrad *et al.* (1964) as providing unequivocal evidence that there is a physical constraint to food intake. The ability of food intake to be accurately predicted from liveweight, faecal output and digestibility is considered to be an artefact.



The work of Conrad *et al.* (1964) proposes that on poor quality foods dry matter intake (DMI) can be predicted from three variables, liveweight (W), digestibility (D) and faecal dry matter output (FO). It is evident, however, that the variables of the model are not independent (Tolkamp, 1999). Digestibility cannot be calculated without knowledge of measured dry matter intake (DMI) and faecal dry matter output (FO);

$$D = (DMI - FO)/DMI$$

Thus, predicted DMI can be completely calculated from a knowledge of total FO (determined from body weight and faecal dry matter) and D so that

$$DMI = FO/(1/(1 - D))$$

DMI, FO and D are therefore not independent of one another, knowledge of any two allows the third to be calculated. Information about digestibility and faecal output will by definition allow dry matter intake to be calculated completely, irrespective of food quality (Grover, 1987; Tolkamp, 1999). The model of Conrad *et al.* (1964) is not therefore specific to high bulk foods and thus cannot be seen to provide unequivocal evidence that there is a physical constraint to intake on bulky foods.

If DMI is modelled correctly (as described above), the effect of weight on intake is nil. The model of Conrad *et al.* (1964) includes liveweight as a variable and what's more DMI is shown to be proportional to liveweight. DMI was predicted from

$$DMI = a \cdot W^{0.99} \cdot D^{1.53} \cdot F^{1.01} \quad (\text{kg/day})$$

where W is liveweight, D is digestibility and F is faecal output (FO)/1000kg W. The use of the variable F means that the model can be rewritten as (Tolkamp, 1999)

$$DMI = a \cdot W^{0.99} \cdot D^{1.53} \cdot ((1000 \cdot FO)/W)^{1.01} \quad (\text{kg/day})$$

Which is equivalent to

$$\text{DMI} = a' \cdot W^{(0.99-1.01)} \cdot D^{1.53} \cdot \text{FO}^{1.01} \quad (\text{kg/day})$$

and the effect of W on DMI becomes nil. Therefore, this model cannot be said to provide evidence that DMI is proportional to liveweight (W). The correct prediction for DMI from D and FO is given above. If this is the case and the effect of W on DMI is nil, then for given D, DMI must be directly proportional to FO (Tolkamp, 1999) which indeed Conrad *et al.* (1964) found it to be. For a given FO Conrad *et al.* (1964) described the effect of D on DMI not correctly as that given above ( $1/(1-D)$ ) but using  $a' \cdot D^{1.53}$ .

For a given set of parameters, the model of Conrad *et al.* (1964) is able to describe the effect of D on DMI for a given FO accurately, but only over a narrow range of digestibilities (Conrad *et al.*, 1964; Tolkamp, 1999). For example, using the parameters quoted in the paper the model can accurately predict the effect of D on DMI for a digestibility range of 0.52 – 0.67 only. The accuracy of the model is significantly reduced when it is used to predict the effect of D on DMI for digestibilities out with this range, unless the parameter values are altered. By changing the parameter values the model can provide accurate predicts over another narrow digestibility range, but, one set of parameters will not provide accurate predictions of the effect of D on DMI over the whole digestibility range (Tolkamp, 1999).

Therefore, the model of Conrad *et al.* (1964) can accurately describe the DMI of cows over a limited digestibility range, but it does not provide specific evidence that food intake is physically constrained. The variables of the model are not independent and no significance can be added to the role of liveweight in the model.

#### 1.3.3.3 *IS PERFORMANCE MAXIMISED?*

The commonly held view, and that used here, is that food intake is aimed at maximising performance. If the assumption of maximisation is correct then the idea

of constraints is a logical one. However, there exists some doubt as to whether or not animals ever really grow as fast as they can as animals are often seen to eat to perform below their potential (Ketelaars and Tolkamp, 1991; Poppi *et al.*, 2000). Such doubts have arisen from observations of for example, compensatory growth. Here after a period of inhibited growth, growth rate exceeds the 'normal' rate expected of an animal allowed to progress along its natural growth curve (e.g. Wilson and Osbourn, 1960; Cole *et al.*, 1968; Owen *et al.*, 1971; Mersmann *et al.*, 1987; Stamataris *et al.*, 1991). From an evolutionary point of view the idea that animals accept a submaximal growth rate may make sense. Although an increased growth rate may have advantages (for example, earlier sexual maturity and breeding), it also carries disadvantages (for example, needing an increased grazing time, which leads to an increased risk of predation).

Although the idea that animals have a genetically determined potential for protein retention and a desired rate of lipid deposition, which determine food intake seems to be a sensible one that is useful for interpreting food intake responses, observations such as those described above suggest that normal growth is not truly maximal and also bring into question whether or not it is possible to accurately predict 'potential' growth.

## **1.4 MAXIMISATION OF EFFICIENCY**

In 1992, Ketelaars and Tolkamp published a series of three papers critically examining current ideas about the causes of differences in voluntary food intake in ruminants. They evaluated the experimental data commonly used to support the idea that animals eat to achieve maximum performance unless limited by gut fill and concluded that this framework '*offers an incomplete and unsatisfactory explanation for the observed variation in intake*'. Pittroff and Kothmann (1999) who after reviewing the original literature concluded that the idea of a physical limitation to food intake '*should be rejected*' echoed this opinion. The concept of maximum performance subject to constraints fails to adequately account for the variation in the

food intake of ruminants fed medium or poor quality foods (as discussed above). Experimental evidence showing a decline in rumen fill with an increase in net energy intake (Weston, 1985, 1996) or an increased rumen fill in lactating cows compared to dry cows (e.g. Weston, 1982) goes against the concept of physical regulation where fill is supposed to be constant. Although the idea that animals will aim to eat at level that will allow genetic potential to be achieved seems to be sensible, animals are often seen to eat at levels below that required for maximal growth (Poppi *et al.*, 2000). Is it therefore correct to assume that animals are intake rate maximisers?.

It was following an increasing dissatisfaction with this concept, particularly with respect to variation in food intake in ruminants, from a number of authors (e.g. Grovum, 1987; Ketelaars and Tolkamp, 1992; Stanley *et al.*, 1992, Pittroff and Kothmann, 1999) that Tolkamp and Ketelaars (1992) produced an alternative framework for the prediction and understanding of food intake in animals. The framework was developed in ruminants but is assumed by the authors to be general and so – if correct – will also apply to monogastrics, although its applicability to monogastrics has yet to be tested.

The framework of Tolkamp and Ketelaars (1992) was developed from an evolutionary perspective where it is thought more logical for feeding behaviour to be aimed at enhancing survival and reproductive success rather than maximising production (Tolkamp and Ketelaars, 1992). If it is assumed that in general food intake has not just benefits but also inherent costs to the animal then the idea that ‘*an optimum intake may exist resulting from a balance between the costs and benefits of food consumption*’ is reasonable (Tolkamp and Ketelaars, 1992). For non-reproducing animals, net energy consumption for maintenance and gain is considered to be the benefit of food intake and the concomitant consumption of oxygen is thought to be the cost. The use of oxygen by the tissues indirectly causes an accumulation of damage to cells, which ultimately results in a loss of vitality, ageing and a limited lifespan (Tolkamp and Ketelaars, 1992). As the net energy intake of a food increases there will be a simultaneous increase in oxygen consumption. As the total amount of oxygen consumed in an animals life is thought to be constant

(Tolkamp and Ketelaars, 1992), it is hypothesised that animals will try to maximise the efficiency of oxygen utilisation, hence for each food *'optimum feed intake is the level of feed consumption at which benefits (kJ of net energy intake) obtained per unit of costs (one litre of oxygen consumed) becomes maximal'*.

According to this framework each food will have a specific optimum level of food intake at which maximum efficiency will be achieved, feeding behaviour will be aimed at achieving this level of intake. Thus, the reduction in food intake on high bulk foods is because the level of net energy intake at which maximum efficiency is attained is reduced as the bulk content of the food increases (Figure 1.3).

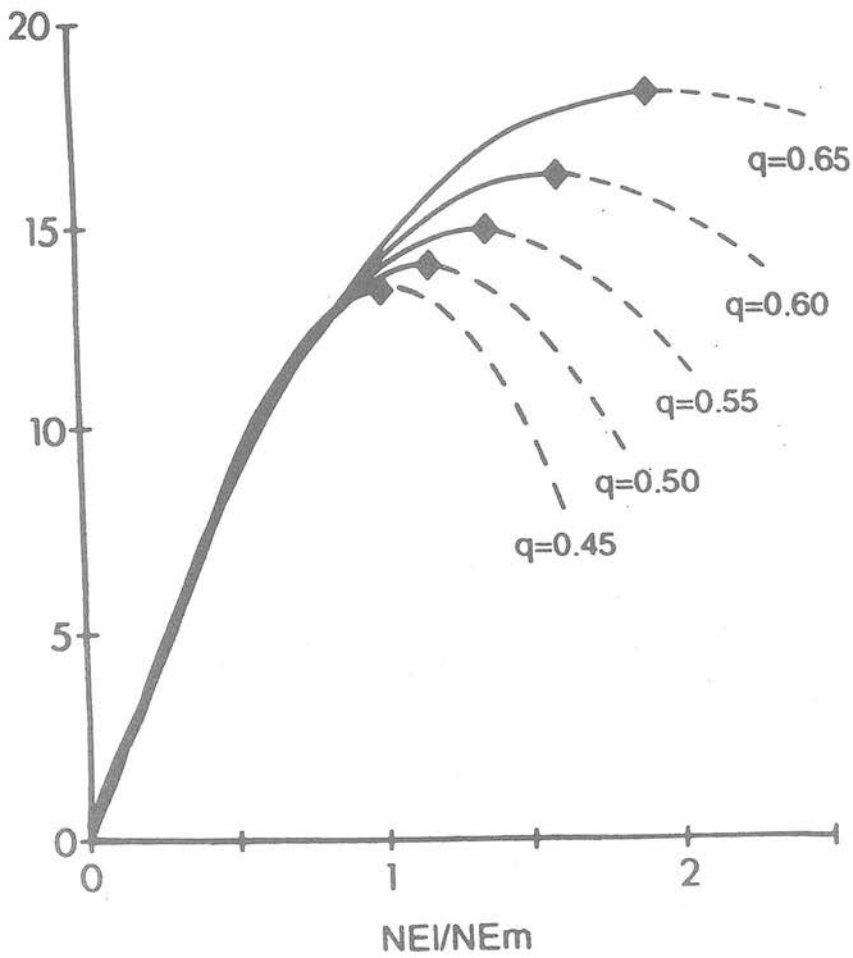
One of the advantages of the framework of Tolkamp and Ketelaars (1992) is that, in contrast to the idea that animals aim to maximise performance subject to constraints, it does not invoke two separate underlying mechanisms for the control of food intake on high and low bulk foods.

### **1.4.1 CRITIQUE OF FRAMEWORK 2**

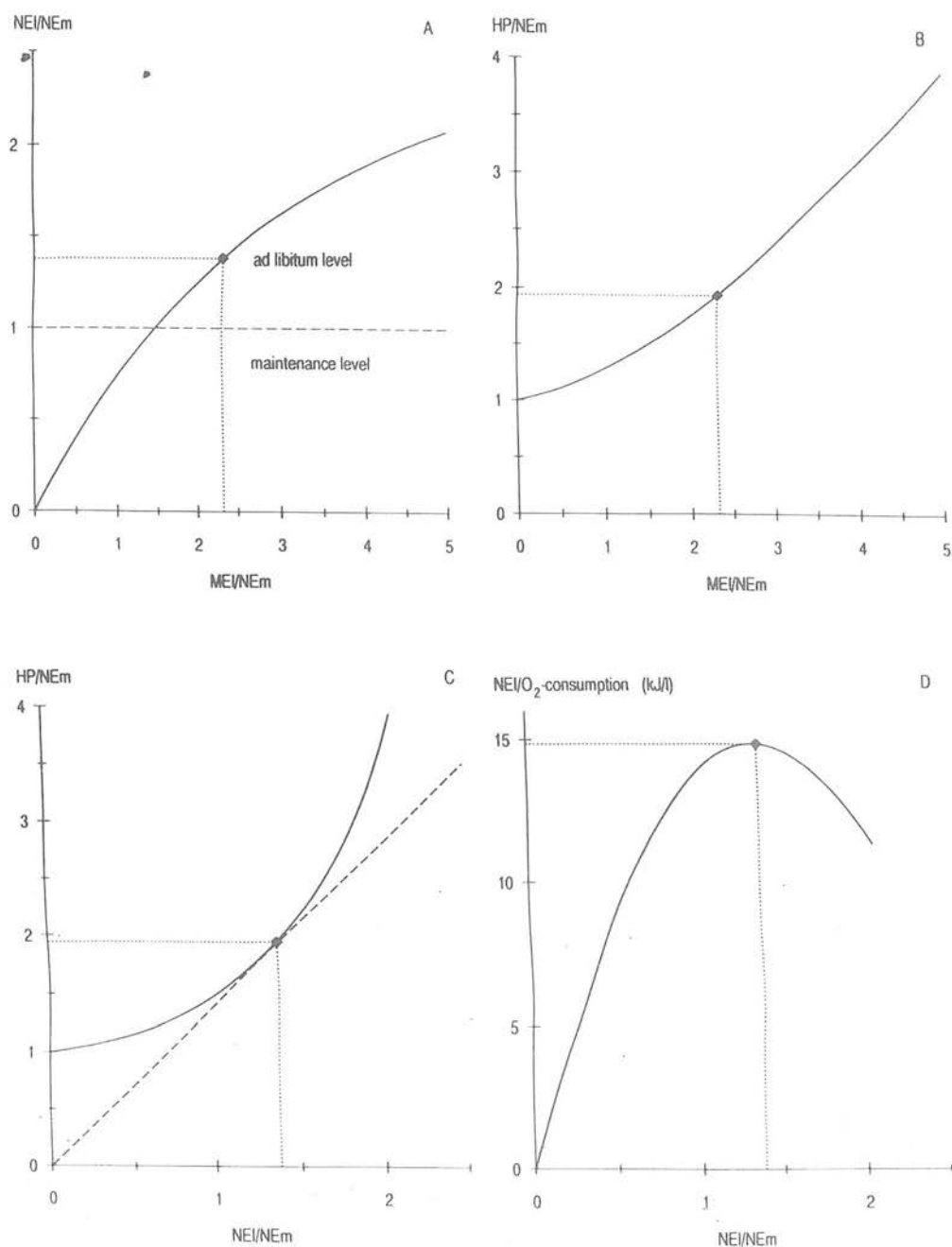
#### ***1.4.1.1 THE MARGINAL EFFICIENCY OF ENERGY USE***

Crucial to the efficiency framework of Tolkamp and Ketelaars (1992) is the assumption that the relationship between food intake and energy retention above maintenance is curvilinear (Blaxter and Boyne, 1978), i.e. that the marginal efficiency with which energy is used above maintenance is diminishing. If this assumption of diminishing marginal efficiency is correct then there can be an 'optimum' level of food intake (see Figure 1.4).

NEI/O<sub>2</sub> - consumption (kJ/l)



**Figure 1.3.** The efficiency of oxygen utilisation (NEI/O<sub>2</sub>-consumption) as a function of NEI for roughages of metabolisability  $q = 0.45$  to  $0.65$ . The (◆) depicts the values corresponding to the average observed voluntary food intake of such foods in sheep. All according to ARC (1981). Where the curves are continued beyond the marked points they are shown as dotted as, in principle, they cannot be observed. Taken from Emmans and Kyriazakis (1995), Figure 1.



**Figure 1.4.** NEI as a function of MEI (a); heat production (HP) as a function of MEI (b); heat production as a function of NEI (c) and the efficiency of oxygen utilisation (NEI/O<sub>2</sub> consumption) as a function of NEI (d). NEI, MEI, HP and O<sub>2</sub> consumption have been scaled to net energy for maintenance (Ne<sub>m</sub>). All data apply to roughages of metabolisability of 0.55. Individual points on the curves depict values corresponding to the average observed voluntary intake of such foods in sheep. All according to ARC (1981). Taken from Ketelaars and Tolkamp (1991), Figure 3.2 p56.

The assumption of diminishing marginal efficiency forms the basis of several energy requirement systems (e.g. ARC, 1981; Blaxter, 1989 and more recently, NRC, 2000). However, in recent years it has been criticised. Firstly, there is no *a priori* reason for this assumption to be correct (Emmans, 1995; Emmans and Kyriazakis, 1995a). The work of Blaxter and Boyne (1978) was not tested in any formal way and no proper justification was given for making the assumption that the relationship between energy and food intake was curvilinear. Prior to the work of Blaxter and Boyne (1978), Blaxter and Wainman (1961) had concluded that energy retention was a linear function of energy supply of two intersecting lines of different slope above and below maintenance. Therefore the marginal efficiency with which energy is used above maintenance was made constant. A linear model assuming constant marginal efficiency has been shown to be able to describe experimental data as well as, if not better, than a curvilinear model assuming diminishing marginal efficiency (Emmans, 1994; 1995; Emmans and Kyriazakis, 1995).

Food intake can have an optimum level (as advocated by Tolkamp and Ketelaars, 1992) only if the assumption of diminishing marginal efficiency is correct. If the marginal efficiency with which energy is used above maintenance is assumed to be constant then the idea that food intake has an optimum level cannot be upheld.

#### *1.4.1.2 THE RELATIONSHIP BETWEEN INTAKE AND OXYGEN EFFICIENCY*

When the equations of ARC (1981) were used to calculate the predicted oxygen efficiency as a function of the scaled dry matter intake (Emmans and Kyriazakis, 1995) it was shown that large changes in dry matter intake resulted in only small changes in efficiency. Dry matter intake could be varied by very large amounts without any adverse effects on efficiency (Emmans and Kyriazakis, 1995). Control systems are normally precisely regulated. The regulation of food intake itself is such that once mature, animals are able to maintain a constant body weight for prolonged periods of time. The idea that the optimum range of food intake should be so wide does not fit with this observation. It seems unlikely that evolution would have produced a control system that was regulated so imprecisely. However, the effect of



a change in intake on oxygen efficiency is much greater if intake is measured as scaled net energy intake (net energy intake scaled to net energy for maintenance). Here, small changes in intake cause large changes in efficiency (Tolkamp and Ketelaars, 1992). Tolkamp and Ketelaars (1992) argue that, for the animal, net energy intake is more relevant than dry matter intake. Emmans and Kyriazakis (1995) advocate the use of dry matter intake because it is independent of the theory of intake that is being proposed.

#### 1.4.1.3 DEGREE OF MATURITY

The framework of Tolkamp and Ketelaars (1992) is assumed to be general across degrees of maturity. According to ARC (1981) scaling to fasting heat production allows animals of differing sizes to be compared, and it also allows the same animal at different degrees of maturity to be compared. If this scaling rule holds, and animals always eat according to the framework of Tolkamp and Ketelaars (1992), then for a given food scaled food intake is predicted to be constant across degrees of maturity. This leads to the prediction that animals on a food predicted to be eaten at above maintenance at any one liveweight will grow forever (Emmans and Kyriazakis, 1995). This prediction is not one that is held by the idea that animals aim to maximise performance subject to constraints. Here it is predicted that there will be a reduction in intake as a multiple of fasting heat production with increasing maturity. Nor is it upheld by experimental evidence. For example Blaxter *et al.* (1982) and Ketelaars and Tolkamp (1991) both showed that scaled food intake was reduced with increasing maturity. The framework of Tolkamp and Ketelaars (1992) predicts that scaled food intake is reduced with increasing maturity only if there is some systematic change in efficiency as the animal grows (Emmans and Kyriazakis, 1995).

Tolkamp and Ketelaars (1992) were aware that scaled food intake is not constant across degrees of maturity. To account for this they assumed that a change in scaled food intake over time could be attributed to a change in the efficiency of ME utilisation '*a decrease in optimum NEI/NE<sub>m</sub> (their measure of efficiency) with*

*increasing weight of the animal must be attributed to a lower efficiency of ME utilisation*'. However, the evidence to support this hypothesis is poor. The data of Graham (1969) provides some support in favour of the idea that the efficiency of ME utilisation decreases with degree of maturity (Ketelaars and Tolkamp, 1996). In contrast, Blaxter *et al.* (1966), who measured efficiency in animals over a four-fold weight range (70 - 289kg), concluded that growing steers used the energy supplied by a diet of constant composition with constant efficiency and that efficiency was consistent with that seen in nearly mature animals on similar foods. Blaxter *et al.* (1982) concluded that the efficiency of energy utilisation was more or less constant in sheep over a weight range of 30 - 130kg. Despite this Tolkamp and Ketelaars (1992) concluded that the evidence on this matter was '*inconclusive*'. They dismissed the work of Blaxter *et al.* (1966) because the experiments used animals that were '*still far from mature weights*', and considered that the estimates of NEm (net energy for maintenance) made by Blaxter *et al.* (1982) (which were used to determine that the efficiency of ME utilisation in sheep was constant) were extremely high, leading the authors to an erroneous conclusion. Emmans and Kyriazakis (1995) considered their dismissal of the available evidence as '*unjustified*'.

#### 1.4.1.4 GENERAL COMMENTS

A major limitation of the framework of Tolkamp and Ketelaars (1992) is that it has only been quantified for mature, non-reproducing animals. Although it shows good quantitative agreement with observed data sets (Tolkamp and Ketelaars, 1992; Ketelaars and Tolkamp, 1996), quantification for other species and physiological states has not been completed. Further, quantification would be a complex process and would require detailed studies on oxygen consumption and energy retention to be completed. Part of the problem with this framework is that efficiency beyond *ad libitum* intake cannot be observed without the aid of force-feeding. It is therefore difficult to determine, other than hypothetically, the shape of the efficiency curve

beyond the point of *ad libitum* feeding. Tolkamp and Ketelaars (1992) assume that beyond *ad libitum* levels efficiency will fall; testing this would be difficult.

It must also be questioned whether or not the evolutionary principles on which Tolkamp and Ketelaars (1992) based their framework are still relevant in today's intensive pig and poultry industry's where animals have been bred for the main purpose of maximising production. The idea of optimisation follows on from the idea of Darwinian evolution and the presumed idea that animals are bred to optimise fitness over a prolonged period of time. Optimisation accounts for the idea that feeding behaviour is aimed at enhancing survival and reproductive success rather than maximising production. The framework of Tolkamp and Ketelaars (1992) is based upon the assumption that animals have a long-term optimal production goal. However, today's modern pig genotypes have been bred to maximise production in the short term and longevity has not been part of the selection goal. While the idea of optimisation may still be relevant in less intensive production systems such as those used for ruminant production, its relevance to the highly intensive pig production industry must be questioned and tested.

If the framework of Tolkamp and Ketelaars (1992) were substantiated then the whole system for predicting food intake would need to be completely rethought which would be no easy task. Although the idea that animals aim to maximise some 'efficiency' is an attractive one, there is some doubt as to whether or not the efficiency in question is the rate of net energy intake per litre of oxygen consumed as suggested by Tolkamp and Ketelaars (1992). Scientific progress is based upon changes in concepts and new ideas. The work of Tolkamp and Ketelaars (1992) is one of few attempts to find an alternative explanation for feeding behaviour and it has shown that there may be other viable frameworks that can account for differences in food intake.

## **1.5 DISTINGUISHING BETWEEN THE FRAMEWORKS**

### **1.5.1 WHY DO WE NEED TO DISTINGUISH BETWEEN THE FRAMEWORKS?**

The idea that animals aim to achieve a desired food intake subject to the presence of a constraint implicitly assumes that the constraint to food intake is inflexible. For example, on high bulk foods when the maximum capacity to consume food bulk is reached food intake is predicted not to be increased further regardless of changes that may occur in the environment or physiological state. However, it has been shown that ruminants have an enormous flexibility in their capacity to deal with high bulk foods. The idea of constraints to food intake cannot account for such flexibility in intake. There is also some question over the validity and interpretation of experimental evidence often cited as being in favour of the idea of a physical constraint to food intake. Preconceived ideas about an experiment can often, unwittingly, lead to an experiment being reported in favour of those preconceptions, even though those preconceptions may be incorrect. The impartial and objective interpretation of scientific results, although aspired to, is difficult to achieve. It is possible that preconceived ideas about the control of food intake may have led to a favourable interpretation of the experimental data considered to provide evidence in favour of a bulk constraint (e.g. Balch and Campling, 1962; Welch, 1967). When viewed from a different perspective (e.g. Grovum, 1987; Ketelaars and Tolkamp, 1992), the experimental evidence is, perhaps, not as conclusive as initially assumed.

The usefulness of the information that is obtained from science depends to large extent on the concepts that are used to generate the questions and to design and interpret the results of experiments. The current framework of food intake control and prediction has been used to generate a large number of questions and apparently provides an appropriate interpretation for an array of responses. Despite this the control of food intake is still poorly understood. Progress in science is made through the testing, criticism and improvement or rejection of current ideas and through the development and testing of new ideas and theories. Changes in scientific concepts

form the basis of scientific progress. Despite this, scientific progress in the development of frameworks that allow food intake to be accurately understood and predicted has been slow. There is still the need to question, criticise and if necessary reject the idea that animals aim to achieve a desired food intake subject to the presence of constraints. The work of Tolkamp and Ketelaars (1992) criticises and then rejects the current framework, before offering an alternative to it. Like all new theories, that of Tolkamp and Ketelaars (1992) also needs to be tested, criticised and either improved or rejected.

Prediction of a system requires an understanding of the underlying biological processes of that system, and accurate models of food intake prediction need to be based upon accurate theories of food intake. It is important to distinguish between the idea that animals aim to achieve a desired food intake subject to constraints and the idea that animals aim to maximise biological efficiency (Tolkamp and Ketelaars, 1992). The repercussions of the idea that animals maximise biological efficiency, for food intake prediction methods are huge. Continued use of the idea that animals have a desired food intake which is limited by constraints, for interpreting variation in food intake will not require any fundamental changes in food intake prediction system, although there exists the need to improve the prediction of food intake on high bulk foods. If, on the other hand, the optimisation framework of Tolkamp and Ketelaars (1992) was adopted as the basis of food intake prediction models the whole food intake prediction system would need to be re-established. This would be daunting in scientific, financial and human resource terms and should not be undertaken lightly. There is, perhaps, therefore, a reluctance to accept fundamental changes to the current system.

The development of new ideas and the critical testing of those ideas is essential for the progress of science. The critical testing of new ideas forms the basis of this thesis. There is some concern over the ability of the current theory for the control of food intake (the idea that animals aim to achieve a desired food intake subject to the presence of a constraint) to account for variation in food intake on poor quality

foods. If this theory is incorrect then any alternative theory needs to be critically tested and either improved or rejected.

### **1.5.2 DIFFERENCES IN THE PREDICTIONS OF THE TWO FRAMEWORKS**

The framework based on the idea that animals aim to achieve a desired food intake subject to the presence of constraints, and that based on the idea that animals aim to optimise food intake so that maximum efficiency is achieved, have very similar predictions of food intake on a high quality control food under a range of conditions (see for example Mertens, 1994). One of the important differences between the frameworks is that they differ in their predictions of the effects that poor quality (high bulk) foods will have upon food intake. This difference stems from the fact that the current framework sees food intake on poor quality foods as being a function of the type food consumed. The optimisation framework developed by Tolkamp and Ketelaars (1992) is based upon the assumption that animals will try to maximise the ratio net energy intake per litre of oxygen consumed. Food intake on poor quality foods (like that of high quality foods) will therefore, be at the level that allows maximum efficiency to be achieved. Based on this assumption food intake on high bulk food will therefore be modified, not dictated by the type of food consumed.

This difference between the frameworks means that under a particular set of environment conditions the frameworks produce contrary predictions for the effect of feeding a high bulk food on food intake, which can be tested by experimentation.

### **1.5.3 HOW CAN THESE DIFFERENCES BE TESTED?**

#### **1.5.3.1 DIFFERENCES IN LONGER TERM FOOD INTAKE**

A severe test of the frameworks can be achieved through experimentation because the frameworks differ in their predictions of food intake on high bulk foods. Specifically the frameworks differ in their predictions of the effect that a reduction in

temperature and a period of reduced growth will have upon the food intake of foods with a high bulk content (see Chapters 2 and 3). Experiments to test these predictions can be designed and comparison of the results from the experiments with the predictions set forward by each framework will determine the framework most appropriate for the prediction and understanding of food intake.

Because the frameworks make similar predictions of food intake on a high quality, low bulk food under a range of conditions it is essential that the high bulk used in these tests are constraining. That is they must limit the growth of the pigs to which they are fed.

#### *1.5.3.2 DIFFERENCES IN SHORT TERM FEEDING BEHAVIOUR*

The measurement of short term feeding behaviour (STFB) is considered to be relevant for the understanding of the control of food intake in the longer term (Forbes, 1985). STFB consists primarily of short feeding bouts or visits to the feeder during which food is consumed. Visits, which are separated by short intervals, are clustered into bouts or meals that are separated by longer intervals (Bigelow and Houpt, 1988; de Haer and de Vries, 1993). Thus, average daily food intake is, in a purely formal sense, the product of the number of meals made in a day and the average meal size. Changes in food intake will therefore reflect changes in meal size, meal number or both. It might therefore be expected that the feeding of a high bulk food, which is limiting to food intake, would be reflected by changes in STFB. Indeed it has been shown that feeding of bulky foods reduces feeding rate and increases total daily feeding time (Brouns *et al.*, 1997; Rushen *et al.*, 1999; Ramaekers *et al.*, 1999).

Information about the way in which STFB changes with a change in food type may provide an insight into the underlying factors that are important for the control of food intake on high bulk foods. For example, if a bulk constraint operates it might be expected that that there would be less diurnal variation in feeding, feeding would

be expected to occur more frequently during the day and perhaps even be extended in to the night. In addition, a change in food to one of higher bulk content would be expected to cause a change in food intake, which would be reflected, by a change in STFB.



## 1.6 AIMS OF THE THESIS

The experiments and ideas presented within this thesis are directed towards improving the prediction of the voluntary food intake of growing pigs on poor quality foods. Within this overall context the specific objectives of the thesis were:

- (i) To provide a severe test of the two frameworks currently available for the prediction and understanding of food intake (**Chapters 2, 3 and 4**). Accurate food intake prediction requires accurate theories of food intake and so it is important to distinguish between the current frameworks. Experiments were designed that tested areas where the frameworks differed in their predictions of food intake on high bulk foods
- (ii) To improve current methodologies for the prediction of food intake on poor quality foods. The objective here was to determine whether or not scaling rules for the prediction of constrained food intake developed in young growing pigs were appropriate for use in larger pigs. A further objective here was to investigate the effects of maturity on the adaptation to bulky foods (**Chapter 5**). Capacity for bulk is expected to change with increasing maturity, but this needs to be investigated.
- (iii) To develop a model that would predict food intake during the adaptation period when there is a change in food to one of higher bulk content (**Chapter 6**). Most models of food intake do not consider the period of adaptation when there is a change to a food of higher bulk content. The adaptation period has important implications for intake and performance on bulky foods. If the extent to which intake and performance will be reduced and the length of the adaptation period can be predicted then this will allow more accurate food intake prediction models to be developed.

# **CHAPTER 2**

**Tests of two theories of food intake  
using growing pigs: 1. The effect of  
ambient temperature on the intake of  
foods of differing bulk content**

## **2.1 ABSTRACT**

An experiment was carried out on pigs to provide a severe test of the two current conceptual frameworks available for the understanding and prediction of food intake. Framework 1 assumes that food intake will be that which allows potential genetic performance to be achieved. If this is not achieved then it is because intake is being constrained. Framework 2 sees food intake as being a consequence of a process of optimisation such that biological efficiency (the ratio of net energy eaten to oxygen consumed) is maximised. Both frameworks predict that a reduction in temperature will increase the intake of a high quality food. For a food of low quality Framework 2 predicts that intake will also be increased when temperature is decreased while Framework 1 predicts that it will not. This difference between the predictions of the two frameworks allows them to be distinguished by means of an experiment in which foods of different quality were fed at different temperatures.

Forty pigs were randomly allocated to one of three foods, a control (C) food based on micronised wheat with 13.1 MJ digestible energy (DE) and 232g Crude Protein (CP) per kg fresh food, or one of two high bulk foods. The high bulk foods contained either 65% unmolassed sugar beet pulp (SBP) or 65% wheatbran (WB). Half the pigs were maintained at a thermoneutral temperature of 22°C for fourteen days followed by a cold temperature of 12°C for fourteen days. The other half were maintained at 12°C for a period of fourteen days followed by a temperature of 22°C for fourteen days. Food intake was recorded daily and liveweight twice weekly.

There was a highly significant food x temperature interaction ( $P < 0.001$ ) for food intake. A reduction in temperature resulted in an increase in food intake on C and WB, but had no effect on the intake of SBP. There was a highly significant effect of both temperature and food on intake ( $P < 0.001$ ). A reduction in temperature resulted in a significant increase in intake, intake on WB was higher than that of either C or SBP. There was no overall effect of temperature on liveweight gain although a reduction in

temperature resulted in a non significant increase in the gain of C and reduction in the gain of WB and SBP. There was a highly significant effect of food ( $P < 0.001$ ) on liveweight gain, gain on C was higher than that on either WB or SBP.

The results of the experiment were in agreement with the predictions set forward by the first framework that growing pigs are eating to achieve maximum performance subject to constraints.

## **2.2 INTRODUCTION**

The ability to correctly predict food intake in growing pigs has become more important since the adoption of *ad libitum* feeding regimes; diet formulation and feeding are the keys to profitable pig production. The accurate prediction of the voluntary food intake of pigs fed *ad libitum* is needed to improve response prediction, and to allow the optimisation of diet formulation and feeding strategy. Despite these potential benefits, there are very few general methods for the prediction of food intake (Kyriazakis and Emmans, 1999). Simple attempts to describe quantitatively intake in pigs by regressing food intake on either time or liveweight (e.g., ARC, 1981; NRC, 1987) are inadequate, because of their lack of generality and the absence of any strong theoretical basis (Kyriazakis and Emmans, 1999). In addition to this, most current systems fail to account adequately for the effect of food quality other than by expressing intake as some form of energy. For pigs on poor quality foods Kyriazakis and Emmans (1995) proposed that the water holding capacity (WHC) of the food could be used as a predictor of intake and corroborating evidence on this was obtained by Tsaras *et al.* (1998). However, there exists a need for further research to define more precisely the effect that the bulk content of the diet has upon food intake (Black, 2000).

The dominant framework for predicting food intake, as outlined in Poppi *et al.* (1994), assumes that actual intake will be that set by the first limiting of several constraints. A better assumption is that food intake will be such that the maximum performance set by the genotype is achieved subject to constraints as outlined by Conrad *et al.* (1964) for dairy cows, Emmans (1981) and (1995), for poultry, Black (1984) for sheep and Kyriazakis and Emmans (1999) for pigs. When the potential performance is not achieved it is because intake is constrained by, for example, the bulkiness of the food, or the hotness of the environment. However, the ability of this framework, hence called Framework 1, to predict the food intake of animals on poor quality foods has been

seriously questioned in ruminants by Grovum (1987), Ketelaars and Tolkamp (1992) and Tolkamp (1999). These authors have argued that the idea of constraints on food intake does not account adequately for the observed intakes on foods of moderate and poor quality. Tolkamp and Ketelaars (1992) presented an alternative framework, here called Framework 2, for the prediction and understanding of food intake. Framework 2 was originally developed for ruminants, but was assumed by the authors to be general, and therefore, if correct, should also be applicable to non-ruminants such as pigs. Framework 2 considers food intake to result from some process of optimisation, such as that which allows the maximisation of some efficiency. The efficiency proposed by Tolkamp and Ketelaars (1992) was the ratio of net energy intake to oxygen consumption. Oxygen consumption is seen as a cost of food intake as it is thought to reduce longevity by causing damage to cells, a loss of vitality and ageing (Tolkamp and Ketelaars, 1992). Framework 2 is able to account for some of the anomalies that are present within Framework 1 and shows good quantitative agreement between predicted and observed *ad libitum* food intakes for a particular set of cases for growing ruminants (Tolkamp and Ketelaars, 1992). An advantage of Framework 2 is that it does not invoke two separate underlying mechanisms in the control of food intake on high and low quality foods.

Although both frameworks predict similar effects of temperature upon the intake of high quality foods, they differ radically in their predictions of the effect of temperature upon the intake of poor quality foods. The aim of the experiment reported here was to provide a severe test of the abilities of these two frameworks to predict the intakes of pigs offered access to poor quality foods at different temperatures. Both frameworks agree in predicting that a reduction in temperature will cause an increase in the intake of a high quality food. However, they differ in their prediction of the effect of a reduction in temperature on the intake of foods high in bulk. Framework 1 sees food intake on a limiting bulky food as a function of the type of food only, and predicts that it will be independent of the climatic environment. Where the intake of a high bulk food is

constrained at a thermoneutral temperature, it is predicted not to increase when temperature is reduced. Framework 2 sees food intake as a function of both the type of food and the climatic environment. It predicts that when temperature is reduced there will be an increase in food intake regardless of the type of food being fed. By giving pigs foods of different quality at different temperatures we hoped to be able to distinguish between the two frameworks.

## **2.3 MATERIALS AND METHODS**

### **2.3.1 ANIMALS AND HOUSING**

Forty pigs were placed immediately after weaning, at 4 weeks of age, into individual pens of the experimental unit. The pigs were 20 entire male Manor Meishan pigs (PIC Group, U.K, 50% Landrace, 25% Large White and 25% Meishan (Mx)), 10 entire male F1 (PIC) hybrids and 10 female F1 (PIC) hybrids (Large White X Landrace X Duroc (LWx)). The average weaning weight of the pigs was 8.0 kg (s.d. 0.57kg) and 9.0 kg (s.d. 1.7kg) for the Mx and LWx animals respectively.

The experimental unit consisted of two identical rooms separated by a central working area. Each room housed 20 pigs in two opposing lines of 10 individual pens, each with its own water supply and metal feeding trough. Underneath each trough a metal tray was placed to collect food spillage. Each room had its own lighting, heating and ventilation system.

### **2.3.2 EXPERIMENTAL FOODS**

Three foods were formulated and made into pellets 3mm in diameter. The control (C) food was based on micronised wheat and had 13.1 MJ digestible energy (DE) and 232g Crude Protein (CP) per kg fresh food. The two high bulk foods were based on either wheat bran (WB) or unmolassed sugar beet pulp (SBP). WB had 10.1 MJ DE and 165g CP per kg fresh food, and SBP had 10.8 MJ DE and 128 g CP per kg fresh food. The two high bulk foods were supplemented with synthetic amino acids and with minerals in order to maintain similar calculated ratios of the essential amino acids and minerals to DE as the control food. The control food was formulated to have low contents of indigestible matter and bulk as measured by water holding capacity (WHC). The



intention was to provide a comparison between one material, sugar beet pulp, which was highly digestible but with a high WHC value, and another, wheatbran, which was less digestible but with a low WHC value (Tsaras *et al.*, 1998; Brouns *et al.*, 1991; Brouns *et al.*, 1995). The control food C was intended not to be limiting while the high bulk foods were intended to limit the growth rate of pigs of the weight used. The WB food was expected to be less restrictive than the SBP food.

The foods were analysed for gross energy (GE), dry matter (DM), crude protein (CP), diethyl ether extract, ash, crude fibre (CF), acid detergent fibre (ADF; Goering and Van Soest, 1970) and neutral detergent fibre (NDF; Robertson and Van Soest, 1977), water holding capacity (WHC), and viscosity. The WHC was determined by the centrifugation method described by Tsaras *et al.* (1998) and viscosity by the *in vitro* method described by Bedford and Classen (1993). The former was expressed as g of water/g of food and the latter as centipoise (cp, 1cp=0.01 dyne second per cm<sup>2</sup>). The detailed chemical composition of the foods is given in Table 2.1.

**Table 2.1.** *The composition and chemical analysis (g/kg as fed) of the three foods used.*

	Food		
	C	WB	SBP
<b>Ingredients</b>			
Micronised Wheat	712.2	222.6	212.2
Wheatbran	0.0	650.0	0.0
Sugar beet pulp	0.0	0.0	650.0
Fish meal	180.0	56.3	53.8
Sogipro	65.0	20.3	19.4
Mineral/vitamin pre mix	12.5	12.5	12.5
Maize oil	20.0	19.7	19.4
Lysine hydrochloride	2.3	5.3	6.0
DL-methionine	0.2	1.3	2.6
L-threonine	1.3	1.9	3.0
L-tryptophan	0.0	0.0	1.0
Monosodium phosphate	6.5	2.0	19.7
Salt	0.0	1.8	0.0
Limestone	0.0	6.3	0.0
Total	1000.0	1000.0	1000.0
<b>Chemical Composition (g or MJ/kg as fed)</b>			
Dry matter (DM)	874.0	869.0	874.0
Gross energy (MJ/kg)	16.6	16.8	15.2
Digestible energy (MJ/kg)	13.1	10.1	10.8
Crude Protein	231.6	165.1	127.6
Ether extract	48.5	50.7	32.7
Ash	66.9	69.4	90.9
Crude Fibre	17.0	67.3	113.6
Acid detergent fibre	21.4	86.2	139.8
Neutral detergent fibre	74.0	251.1	249.1
Viscosity (centipoise)	9.7	7.9	17.1
Water Holding Capacity (g water/g dry food)	3.49	4.45	8.27

### 2.3.3 EXPERIMENTAL DESIGN

The pigs were randomly allocated to a food, a room within the experimental accommodation and to a pen within their allocated room. Genotype, sex and litter structure were all taken into account during randomisation so that the treatments were balanced for these 3 factors. Allocation to foods was such that 12 pigs (6 of each genotype) were on the control food (C) and 14 pigs (7 of each genotype) were on each of the high bulk foods.

Prior to the start of the experiment the pigs were given 14 days to acclimatise to the accommodation, overcome any post-weaning stress and to allow an average target weight of 12kg to be reached. During this time the pigs were fed a high quality commercial food containing 215g CP/kg (Easiwean, BOCM Pauls Ltd.) *ad libitum*. The temperature was initially set at 25°C and was gradually reduced to 22°C by the start of the experiment. After this 14-day period the experimental foods were introduced. The pigs were given a 10 day period to adapt to the foods. This was slightly longer than the 7 day period recommended by Tsaras *et al.* (1998) because after a 7 day period had passed the intakes of the SBP food were still rather low. The temperature was held at 22°C during the adaptation period.

The experiment was a changeover design that had two experimental periods (Period 1 and Period 2) each of 14 days duration. The temperature was changed over from Period 1 to Period 2 in each room either from 12°C to 22°C (left hand room) or from 22°C to 12°C (right hand room). Temperatures during Periods 1 and 2 were reduced to 12°C, or increased to 22°C, in 3 steps over a period of 3 days (from 22°C to 18°C to 15°C to 12°C or from 12°C to 15°C to 18°C to 22°C). The gradual, stepwise change was used because it was hoped that this would reduce the time taken for the pigs to adapt to the new temperatures. The average temperatures achieved in the right hand room were 22.0 (s.d. 0.43) °C during Period 1 and 12.8 (s.d. 0.62)°C during Period 2. The average

temperatures achieved in the left-hand room were 13.0 (s.d. 1.11)°C and 22.2 (s.d. 0.91)°C during Periods 1 and 2 respectively. Each pig remained on the same food throughout the experiment. A change over design was used to reduce the effects of any variation in food intake between pigs and between the two rooms in the experimental unit. A period of 14 days, according to the results of Kyriazakis and Emmans (1995), was thought to be long enough to monitor any changes in the intake of pigs that have had previous experience of bulky foods, as was the case here. The temperatures chosen for the experiment were intended to be either thermoneutral or cold. A temperature of 22°C is considered to be within the thermoneutral zone for pigs between 10 and 15kgs in weight fed *ad libitum* (Whittemore, 1998). A temperature reduction of 10°C was estimated to allow a potential increase in food intake of 12-15% (Tolkamp, personal communication, 1998).

#### **2.3.4 MANAGEMENT**

All pigs were weighed on the first and last day of each period and twice weekly in between. Weighing occurred at the same time each day, prior to feeding. Food was given twice daily at 09.00 and 16.30 h in order to minimise food spillage, with approximately half the daily allocation being given at each feed. The pigs were fed *ad libitum* with food refusals being maintained at 10-15% of intake. Food spillage from the trays and refusals from the trough were collected daily each morning, weighed and their DM determined by oven drying at 80°C for 24hrs. DM content was then used to determine the fresh weight of the food consumed. Temperature was recorded twice a day, prior to feeding, by minimum - maximum thermometers.

### 2.3.5 STATISTICAL ANALYSIS

The data were analysed for the effects of, and interactions between, food and temperature. The variables analysed were absolute food intake, liveweight gain (LWG), food intake scaled for liveweight (scaled food intake, see below), scaled liveweight gain and food conversion efficiency (FCE). Weight at the start of each period was included as a covariate for the analysis of LWG and food intake only. The data were analysed using Genstat for Windows (release 3.2, Lawes Agricultural Trust, 1993). Residual Maximum Likelihood (REML) was used to account for the unbalanced nature of the data. Pig nested within period was used as the random model; the fixed factors in the model were diet and temperature. Wald tests were used to see if the effects of diet and temperature and their interactions, given by the REML procedure, were significant. Means and standard errors of differences were also obtained from this procedure. Breed and sex had no effect on any of the parameters analysed and so were not included in the final REML model that was used.

For both periods food intake was scaled to liveweight, to take account of any differences in mean weight between treatments. Kyriazakis and Emmans (1995) and Tsaras *et al.* (1998) found that for pigs of 12 - 45kgs on high bulk diets, food intake was directly proportional to liveweight. On the basis of that work it was expected that intake in this experiment would also be directly related to liveweight for a given food in a given environment. This assumption was tested by regressing intake on liveweight for each of the six food/temperature combinations using the final seven days of each period, because the pigs were assumed to have fully adapted to the environmental temperature by this time. In no case was the intercept significantly different to zero (Table 2.2). Therefore the assumption that intake was proportional to liveweight was taken to be appropriate and a scaled rate of intake (SFI) was calculated as g food per kg liveweight per day. The scaling of intake to liveweight allowed for any differences in mean weight between the treatments. Due to the nature of the foods, and because the pigs were maintained at

different temperatures, mean weights of the treatments were different at the end of each period.

Live weight gain was also scaled directly to liveweight. This was done to allow direct comparisons between liveweight gain and scaled food intake to be made.

**Table 2.2.** The intercepts (*a*), regression coefficients (*b*<sub>1</sub>, *b*<sub>2</sub>) and the residual error mean square (REMS) for the regression of feed intake (SFI) on liveweight, for pigs given access to one of three foods at two different temperatures. In Model 1 '*a*' is estimated; in Model 2 '*a*' is assumed to have a value of 0.

Food	Temperature	Model 1 (FI = <i>a</i> + <i>b</i> <sub>1</sub> .W + error <sub>1</sub> )			Model 2 (FI = <i>b</i> <sub>2</sub> .W + error <sub>2</sub> )	
		<i>a</i> (s.e.)	<i>b</i> <sub>1</sub> (s.e.)	REMS	<i>b</i> <sub>2</sub> (s.e.)	REMS
C	22°C	75 (190)	37.00 (6.80)	8076	39.66 (0.967)	7318
C	12°C	759 (447)	22.55 (15.4)	24229	48.55 (1.76)	28778
WB	22°C	-20 (401)	51.73 (14.5)	27508	51.03 (1.54)	25397
WB	12°C	134 (288)	56.12 (10.7)	52311	60.60 (2.28)	48893
SBP	22°C	-143 (313)	43.75 (15.2)	44278	36.89 (2.65)	41585
SBP	12°C	-330 (282)	51.45 (14.4)	34234	34.88 (2.56)	35200

## **2.4 RESULTS**

### **2.4.1 FOOD CHARACTERISTICS**

WHC capacity and viscosity were determined for each of the three foods to provide measures of bulk. The values for these characteristics are given in Table 2.1. Food SBP had the highest WHC (8.27 g water/g food), CF and ADF (114 and 140 g/kg fresh food respectively) and was the most viscous of the three foods (17.1 cp). Food C had the lowest WHC (3.49 g water/g food), but was slightly more viscous (9.7 cp) than food WB. WB was the least viscous of the three foods (7.9 cp), but had a WHC that was between the values for C and SBP (4.45 g water/g food) and the highest content of NDF (251 g/kg fresh food).

### **2.4.2 INITIAL WEIGHT**

The unadjusted raw means for absolute food intake and LWG are given in Table 2.3. An inevitable and expected consequence of the design of the experiment was that pigs on the 3 feeds had significantly different initial weights at the beginning of each Period. On average the pigs fed C, WB and SBP weighed 19.2 (s.d. 2.25) kg, 17.7 (s.d. 2.65) kg, and 14.8 (s.d. 1.81) kg respectively at the beginning of Period 1. At the beginning of Period 2 the pigs fed C, WB and SBP weighed 29.6 (s.d. 3.86) kg, 26.8 (s.d. 3.98) kg and 18.8 (s.d. 2.65) kg respectively; all of these differences were highly significant ( $P < 0.001$ ). As initial weight had a highly significant ( $P < 0.001$ ) effect on absolute food intake and LWG within a treatment, these variables were then analysed with initial weight as a covariate (Table 2.4). Initial weight had no significant effect on FCE and so was not included in the analysis of this variable.

In no case did the 3 breed/sex combinations (male/LWx, female/LWx and male/Mx)

have any significant effect on absolute food intake, scaled food intake, liveweight gain (LWG), scaled liveweight gain (SLWG), or food conversion efficiency (FCE).

#### **2.4.3 EFFECTS ON FOOD INTAKE (FI) AND SCALED FOOD INTAKE (SFI)**

The unadjusted raw means for absolute food intake and LWG, given in Table 2.3, show that both were severely reduced on SBP compared to C. Part of the difference in absolute food intake between the foods can be attributed to differences in initial pig liveweight between the foods. The means for absolute food intake, after adjustment for the covariate, are given in Table 2.4.

The food x temperature interaction was significant for absolute food intake ( $P < 0.05$ ). Temperature affected food intake differently depending on the type of food that was being fed. A reduction in temperature caused a significant increase in the intake of C, but had no significant effect on the intake of either WB or SBP. Intake at 12°C was 1.20 ( $P < 0.05$ ) of that at 22°C for C, 1.10 (ns) of that at 22°C for WB, and 0.91 (ns) of that at 22°C for SBP.



**Table 2.3:** The unadjusted means of daily rate of absolute food intake (FI) and liveweight gain (LWG) of pigs fed one of three foods, control (C), wheatbran-based (WB) and sugar beet pulp-based (SBP), at two different ambient temperatures, high (22°C) and low (12°C).

Temperature	FI (gday <sup>-1</sup> )		LWG (gday <sup>-1</sup> )		FCE	
	22 °C	12 °C	22 °C	12 °C	22 °C	12 °C
Food						
C	1063	1271	734	751	0.674	0.621
WB	1398	1546	800	611	0.554	0.424
SBP	811	780	365	288	0.426	0.418
sed		79.2		97.4		0.056

**Table 2.4:** The adjusted means for daily rate of absolute food intake (FI), liveweight gain (LWG) and food conversion efficiency (FCE) of pigs fed one of three foods, control (C), wheatbran-based (WB) and sugar beet pulp-based (SBP), at two different ambient temperatures high (22°C) and low (12°C).

Temperature	FI (g day <sup>-1</sup> )		LWG (g day <sup>-1</sup> )		FCE	
	22 °C	12 °C	22 °C	12 °C	22 °C	12 °C
Food						
C	978	1190	692	746	0.674	0.621
WB	1327	1459	765	604	0.554	0.424
SBP	1015	933	395	290	0.426	0.418
sed		82.9		95.4		0.056
Effects						
Covariate (initial weight)		***		**		ns
Temperature		***		ns		*
Food		***		***		***
Food*Temperature		*		ns		ns

There was also a highly significant food x temperature interaction for scaled food intake ( $P < 0.001$ ) (Table 2.5). A reduction in temperature caused an increase in the scaled food intake of both WB and C. The scaled food intakes of C and WB at 12°C were 1.14 ( $P < 0.01$ ) and 1.15 ( $P = 0.01$ ) of that at 22°C respectively. There was no significant change in the scaled food intake of SBP when the temperature was reduced from 22°C to 12°C. Making the comparisons of intakes at the two temperatures within animals showed highly significant differences between the three foods. The average increase in scaled food intake at the lower temperature, compared to the higher, was  $4.7 \text{ g kg}^{-1} \text{ d}^{-1}$  (s.e. 1.38,  $P < 0.01$ ) for C,  $7.5 \text{ g kg}^{-1} \text{ day}^{-1}$  (s.e. 0.963,  $P < 0.01$ ) for WB but only  $0.32 \text{ g kg}^{-1} \text{ day}^{-1}$  (s.e. 1.90, ns) for SBP.

The main effects of the type of food offered and temperature need to be seen in the light of the significant interaction between the two factors. Both of the main effects had a highly significant effect on food intake and scaled food intake ( $P < 0.001$ ). Intake was greater for WB and less for SBP than for C. The absolute food intake for C was 0.78, and for SBP 0.70, of that for WB. Scaled food intake for C was 0.75, and for SBP 0.74, of that for WB. Intake was greater at 12°C than at 22°C. Scaled food intake at 22°C was 0.91 of that at 12°C and absolute food intake at 22°C was 0.93 of that at 12°C.

#### 2.4.4 TEMPORAL EFFECTS OF A CHANGE IN TEMPERATURE UPON SCALED FOOD INTAKE (SFI)

The temporal effects that a change in temperature had upon the scaled food intake of each of the three foods are in Figure 2.1. The effect of temperature on the scaled food intake of C (Figure 2.1a) and WB (Figure 2.1b) was almost immediate and initially rapid. By day 17 (the point at which the change in temperature was fully established) the response in food intake was clear. The increase in the scaled food intake of C with a reduction in temperature was fully established by Day 21, while the drop in scaled food

intake with an increase in temperature was established by Day 18. The response of scaled food intake on WB (Figure 2.1b) to a change in temperature is very similar to that seen on C, although there was a much smaller drop in scaled food intake with an increase in temperature on WB than on C. Scaled food intake on SBP did not respond at all to a change in temperature (Figure 2.1c), with the slight increase during the first half of the experiment seen as the pigs adapted to the food.

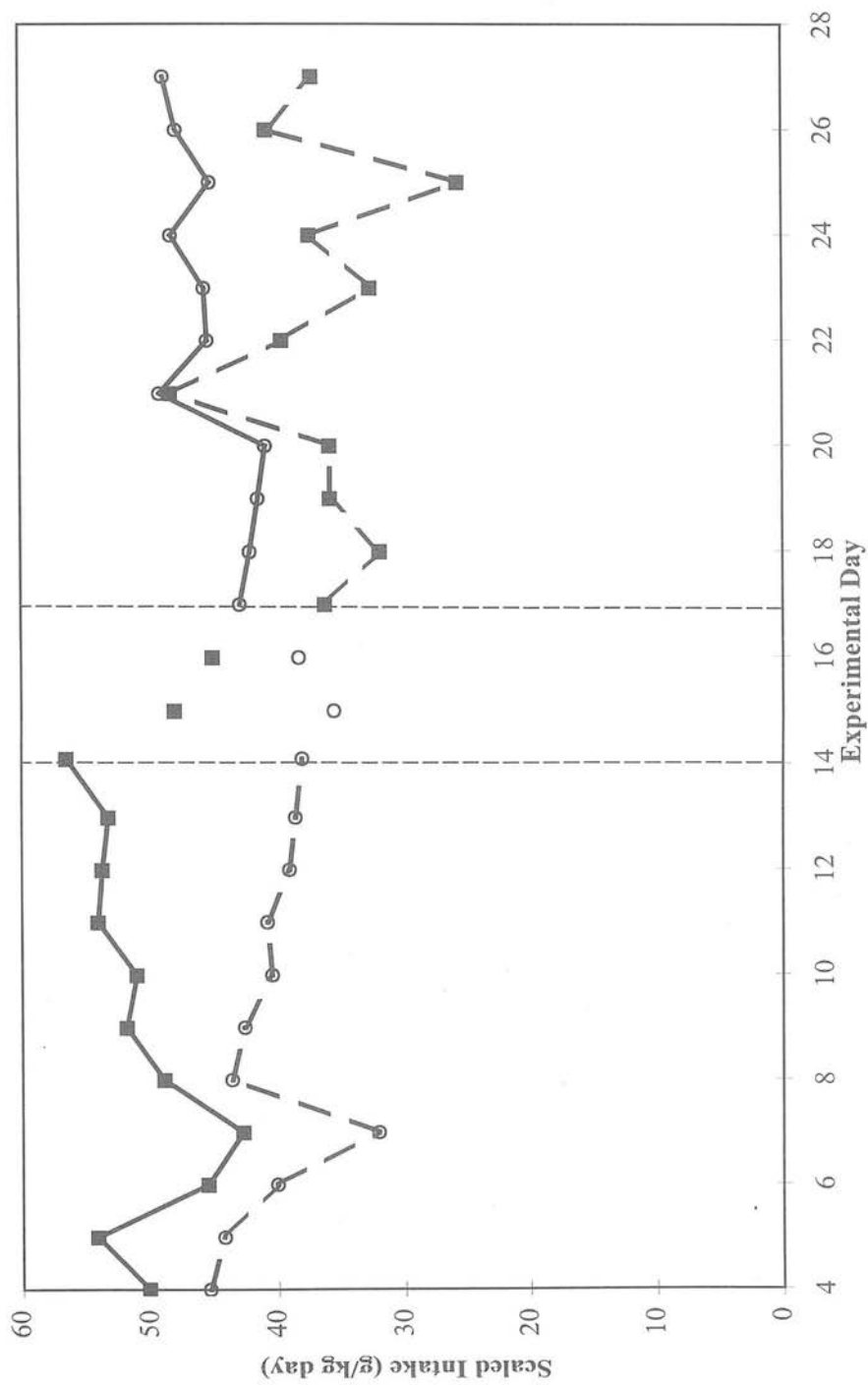
**Table 2.5:** The daily rate of scaled food intake,  $SFI\ g\ kg\ liveweight^{-1}\ day^{-1}$ , scaled liveweight gain ( $SLWG, g\ kg\ liveweight^{-1}\ day^{-1}$ ) of pigs fed one of three foods, control (C), wheatbran-based (WB) and sugar beet pulp-based (SBP), at two different ambient temperatures high ( $22^{\circ}C$ ) and low ( $12^{\circ}C$ ).

Temperature	SFI ( $g\ kg^{-1}\ day^{-1}$ )		SLWG ( $g\ kg^{-1}\ day^{-1}$ )	
	22°C	12 °C	22 °C	12 °C
Food				
C	38.42	43.68	25.14	27.15
WB	50.90	58.44	27.91	24.94
SBP	40.48	40.80	17.10	16.81
sed		2.29		2.58
Effects				
Temperature		***		ns
Food		***		***
Food*Temperature		***		ns

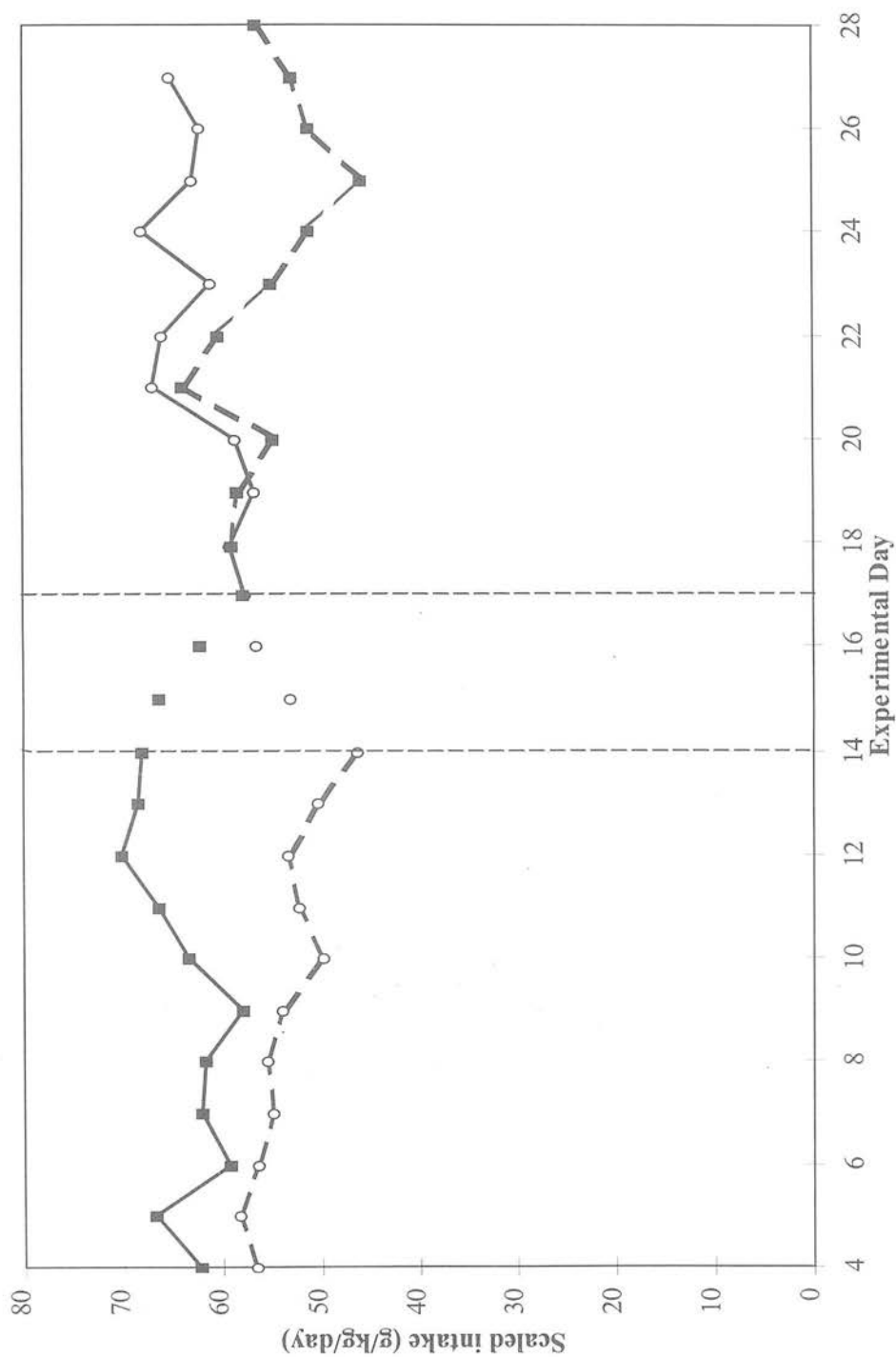
#### 2.4.5 EFFECTS ON LIVEWEIGHT GAIN (LWG) AND SCALED LIVEWEIGHT GAIN (SLWG)

There was no significant food x temperature interaction for LWG or SLWG. The proportional effects of reducing the temperature from 22°C to 12°C on LWG were: an increase of 0.08 for C, a reduction of 0.21 for WB and a reduction of 0.27 for SBP (Table 2.4); despite being large none of these effects was significant. There was no difference in the SLWG of C, a reduction of 0.17 in the SLWG of WB and a reduction of 0.12 in the SLWG of SBP when the temperature was reduced from 22°C to 12°C (Table 2.5). Again, although large, these effects were not significant.

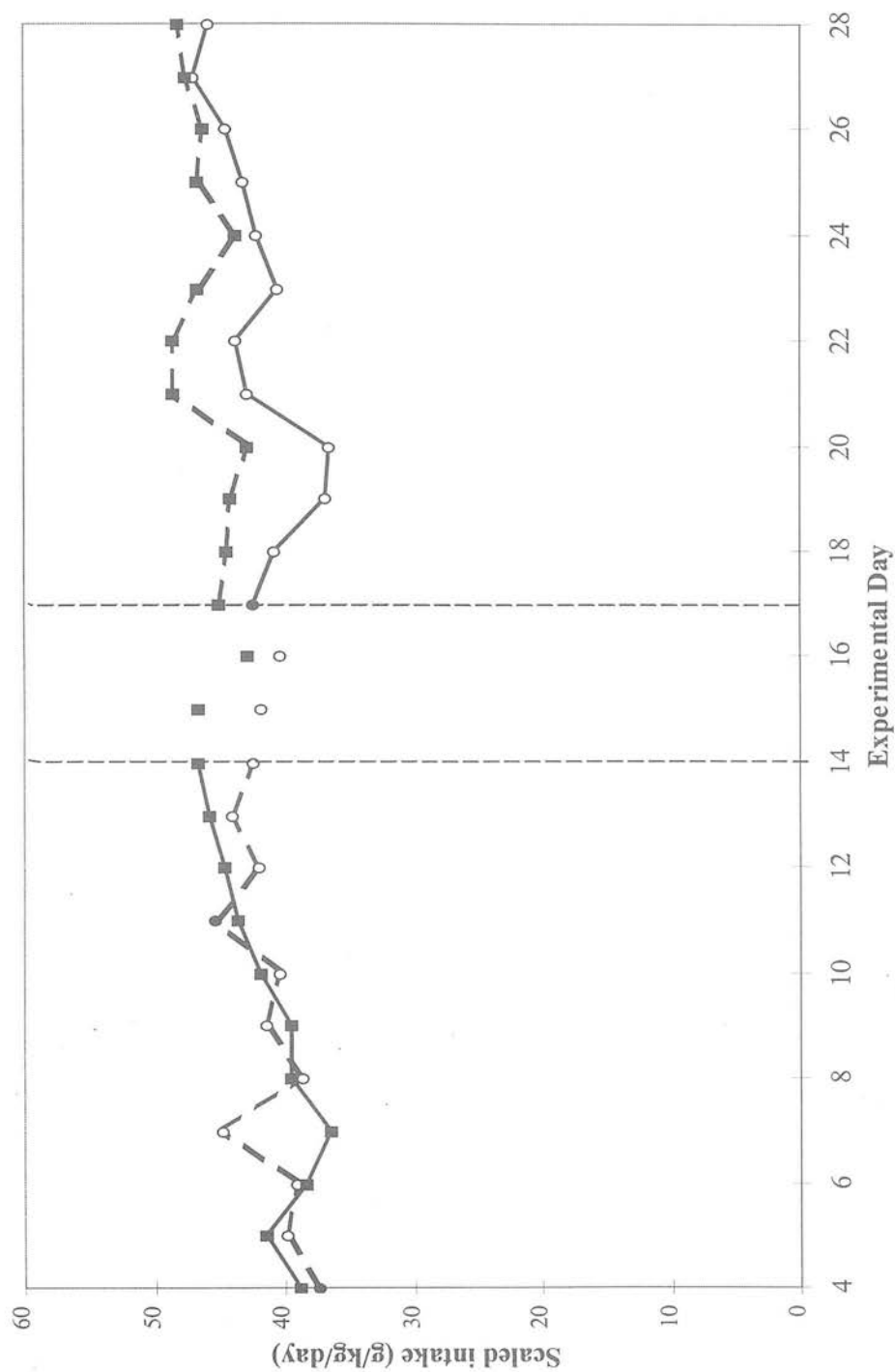
The type of food had a highly significant effect on both LWG and SLWG. Pigs on C grew at 719g d<sup>-1</sup> compared to 685g d<sup>-1</sup> and 343g d<sup>-1</sup> for WB and SBP respectively. There was no difference in the average SLWG of C and WB with values of 26.5 and 26.2g kg<sup>-1</sup> d<sup>-1</sup> respectively. Pigs fed SBP grew by far the slowest with a LWG of 343g d<sup>-1</sup> and a SLWG of 16.9g kg<sup>-1</sup> d<sup>-1</sup>. There was no significant main effect of temperature on either LWG or SLWG.



**Figure 2.1a** The effects of a change in environmental temperature on the Scaled Food Intake (SFI,  $\text{g kg}^{-1} \text{d}^{-1}$ ) of the control food. The dotted vertical lines denote the period of 3 days during which the temperature was changed. The treatments are shown as:  $\square$ — $\square$  for 120°C to 220°C and  $\circ$ — $\circ$  for 220°C to 120°C. Days 1-3 of Period 1 are omitted.



**Figure 2.1b** The effects of a change in environmental temperature on the Scaled Food Intake (SFI,  $\text{g kg}^{-1} \text{d}^{-1}$ ) of the wheatbran food. The dotted vertical lines denote the period of 3 days during which the temperature was changed. The treatments are shown as:  $\square$ — for 120°C to 220°C and  $\circ$ — for 220°C to 120°C. Days 1-3 of Period 1 are omitted.



**Figure 2.1c** The effects of a change in environmental temperature on the Scaled Food Intake ( $\text{SFI, g kg}^{-1} \text{ d}^{-1}$ ) of the sugar beet pulp food. The dotted vertical lines denote the period of 3 days during which the temperature was changed. The treatments are shown as:  $\square$ ----- $\square$  for 12°C to 22°C and  $\circ$ ----- $\circ$  for 22°C to 12°C. Days 1-3 of Period 1 are omitted.



#### 2.4.6 FOOD CONVERSION EFFICIENCY (FCE)

There was no significant food x temperature interaction for FCE. A reduction in temperature caused a reduction in the FCE of all the foods. FCE was significantly reduced ( $P < 0.05$ ) when the temperature was reduced from 22°C to 12°C. Type of food had a highly significant effect ( $P < 0.001$ ) on FCE. FCE was reduced as the energy content of the foods was decreased. Pigs fed C were the most efficient while the pigs fed SBP were the least efficient (0.648 and 0.422 for C and SBP respectively).

## **2.5 DISCUSSION**

Most of the models that are currently available for the prediction of voluntary food intake in pigs do not account adequately for the effect that food quality has upon food intake and there is a lack of good, accurate quantitative methods to predict intake on poor quality foods. In recent years it has been suggested that the idea that animals eat at the level that will allow maximum performance to be achieved, unless food intake is constrained in some way, does not adequately account for the voluntary food intake of ruminants on moderate and poor quality foods. This has led to the development of an alternative framework (Tolkamp and Ketelaars, 1992), so that currently there are now two frameworks available for the prediction and understanding of voluntary food intake in animals. The second framework is based upon the idea that animals eat at a level that allows maximum efficiency to be achieved. The work of Tolkamp and Ketelaars (1992) offers a real alternative to the current framework and may account for some of the anomalies that exist with it, but its generality has yet to be tested. There are important implications of this framework being more general. Food intake prediction models would have to be completely re-thought, and detailed studies on oxygen consumption and energy retention would need to be completed; this would be no easy task.

The objective of the experiment was to provide a severe test, in pigs, of the frameworks currently available for the prediction and understanding of food intake; a non-ruminant animal was considered an easier experimental model than a ruminant to test the two frameworks. The experiment was designed to operate in an area where the frameworks produce different predictions. The frameworks predict the same for the effect of temperature on the intake of high quality, low bulk foods, but differ in their predictions of the effect of reduced temperature on the intake of poor quality, high bulk foods. The basis of this experiment was that the two frameworks of food intake could be distinguished from each other because they predict that a reduction in temperature will

have radically different effects on the intake of a high bulk food. The first framework (maximum performance subject to constraints) predicts that there would be an interaction between food intake and temperature. A reduction in temperature is predicted to increase the intake of a low bulk food but to have no effect on the intake of any high bulk food that limited the performance of growing pigs at a thermoneutral temperature. Once gut capacity has been reached intake is not predicted to be able to increase further with a reduction in temperature. The second framework predicts that a reduction in temperature would increase food intake regardless of the type of food, and that there would be no feed x temperature interaction. At low temperatures on a bulky food the animal will need to oxidise a larger fraction of its metabolisable energy intake in order to maintain body temperature. This will result in a reduction in net energy intake, an increased oxygen consumption rate and, consequently, a reduction in oxygen efficiency if intake remains unchanged. By increasing food intake net energy intake can be increased and efficiency will be improved.

The results of this experiment are in agreement with the predictions set forward by Framework 1. The highly significant food x temperature interaction for food intake in this experiment suggests that under the circumstances of this experiment growing pigs eat to achieve maximum performance unless they are constrained in some way. On a non-limiting food (C) intake was increased in response to an increased energy requirement when the temperature was reduced. On a high bulk food (SBP) there was no increase in food intake with a reduction in temperature suggesting that food intake was being constrained by the bulk content of this food.

The effect of temperature on the food intake of a high quality low bulk food has been well documented (e.g. Lynch, 1989; Close, 1989; Black *et al*, 1999). A reduction in temperature is expected to cause an increase in food intake. The results from this experiment for food C were in agreement with previous work (e.g. Kyriazakis *et al*,

1991; Black *et al.*, 1999); a reduction in temperature from 22°C to 12°C caused an increase in food intake, whilst growth rate was not significantly affected.

The performance of the pigs fed C and SBP was as expected and was comparable to that found in other work (Tsaras *et al.*, 1998). Pigs fed C were assumed to be achieving their potential. However, the performance of the pigs fed WB was much better than had been expected. An inclusion level of 65% wheatbran was expected to limit the performance of pigs of this weight on the basis of the work reported by Kyriazakis and Emmans (1995). However, at the higher temperature used, WB was not a limiting food, as evidenced by growth rates that were comparable to those achieved on C. The pigs fed WB were able to adapt to the food and an increased intake allowed them to compensate for its reduced quality and hence to maintain performance. The WB treatment cannot be seen as providing a severe test of the two frameworks. The predictions set forward by the frameworks for the effect of temperature upon the intake of bulky foods are based upon the assumption that a bulky food is one that limits performance. The frameworks have similar predictions for the effect of a reduction in temperature upon the food intake of non-limiting foods and therefore such a food cannot be used to distinguish between them. The high intake and level of performance on WB could be due to a number of characteristics of this food, of which one is WHC. WHC was considered the main indication of the bulk content of the foods in this experiment. WHC is a measure of a food's ability to hold water. A food with a high WHC can hold more water and so is expected to take up more room in the gastrointestinal tract. Kyriazakis and Emmans (1995) and Tsaras *et al.* (1998) have shown that WHC appears to be able to account for differences in the voluntary food intake of pigs on bulky foods. The WHC of WB was only 1.3 times that of C. For SBP food the WHC was 2.4 times that of C. Our results are consistent with the view that WHC of a food is a property that limits food intake of pigs on bulky foods. On the basis of WHC alone intake on WB would be expected to be only slightly restricting compared to C. Although WB did not reduce growth rate and thus was not a limiting food at the higher temperature, it did however, provide indirect

evidence that is in favour of the first framework. At 12°C WB did appear to be a limiting food. A reduction in temperature caused an increase in intake, but this was not enough to maintain growth rate at the same rate as for C. This suggests that intake on WB was being constrained by the bulk content of the food at 12°C. The reduction in growth rate on WB at 12°C can then be explained by an increase in the amount of heat energy required for cold thermogenesis, compared with 22°C, so that there was a reduced amount of energy available for growth.

There was a rapid response of food intake to a change in temperature. Such a rapid response has been noted elsewhere (Quinou *et al.*, 1997); food intake changed each day as temperature changed. Changes in food intake are generally considered to be a direct response to changes in heat loss associated with changes in temperature and often occur after a delay, particularly when there is a reduction in temperature (Verhagan *et al.*, 1987; Black *et al.*, 1999). The pigs in this experiment were individually penned on slatted floors and physiological, postural and behavioural changes in response to changes in temperature were therefore limited. Under such circumstances changes in food intake must become the most important variable for the control of body temperature and so a rapid response of food intake to changes in temperature would be expected.

It was presumed that if the pigs fed C were cold at 12°C then the pigs fed SBP would be equally or more so. It was expected that for SBP and WB a reduction in temperature would result in food energy being diverted from growth to heat production, and that this would lead to a reduction in growth rate and hence efficiency. Although there was a slight reduction in growth rate of the pigs fed SBP at 12°C compared to 22°C, it was not significant. The current experimental design, and large individual differences between pigs, gave no real means of testing the assumption that the SBP animals were cold at 12°C. It is highly likely that more heat was released from the consumption of SBP than from either C or WB. It has been shown that high fibre foods have a higher heat increment as a result of fermentation by microorganisms in the hind gut (Zhu *et al.*,

1993) and the extra cost of their digestion and metabolism (Lee and Close, 1987). This additional heat will be available to substitute for some of the extra heat required in colder environments (Lee and Close, 1987). The absence of changes in growth rate of the pigs on SBP when the temperature was reduced could be related to changes in the composition of the gain (Verstegen *et al.*, 1973; Verstegen *et al.*, 1982; Close, 1989), pigs can forego some fat growth to provide additional energy for heat production. A small reduction in fat gain would provide a relatively large increase in heat production due to the energy dense nature of fat. Estimates of the composition of the gain could be measured in a slaughter experiment so that the difference in composition at 22°C and 12°C could be compared and contrasted to see if fat growth was indeed less at 12°C.

## **2.6 CONCLUSIONS**

The results from this experiment are in agreement with the predictions set forward by the maximum performance subject to constraints framework. There was a clear food composition x temperature interaction for intake. The experimental design used has succeeded in providing a test of the two current frameworks of food intake and has provided clear evidence in favour of one of those frameworks. On poor quality foods it may therefore be assumed that voluntary food intake of pigs is influenced by the constraint of food bulk in relation to gut capacity. Future experiments need to look at providing further severe tests of these two frameworks by testing other areas where they differ in their predictions of intake on bulky foods.

# **CHAPTER 3**

**Tests of two theories of food intake  
using growing pigs: 2. The effect of  
a period of reduced growth rate on  
the subsequent intake of foods of  
differing bulk content**



### **3.1 ABSTRACT**

The effect of a period of feeding on a high bulk food, upon the subsequent intake of foods of differing bulk content, was investigated in two experiments of the same design. The intention was to provide a severe test of the two current conceptual frameworks available for the prediction and understanding of food intake. In each experiment forty male Manor Meishan pigs were randomly allocated to 1 of 4 treatment groups at weaning. Each experiment was split into 2 periods, P1 (12 - 18kg) and P2 (18 - 32kg). The treatments, all with *ad libitum* feeding, were: a control food (C) fed throughout (treatment CC); a medium bulk food (M) fed throughout (treatment MM); a high bulk food (H) fed in P1 and then C in P2 (treatment HC); H fed in P1 and M in P2 (treatment HM). C was based on micronised wheat with 13.4 MJ digestible energy and 243g crude protein per kg fresh food. In Experiment 1 M contained 35% and H 56% unmolassed sugar beet pulp and in Experiment 2 M contained 50% and H 70% unmolassed sugar beet pulp. Framework 1 predicted that food intake on the medium bulk food (M) would not be increased, whereas Framework 2 predicted that intake on M would be increased after a period of feeding on H, compared to when M was fed continuously.

In P1 both intake ( $P < 0.01$ ) and growth ( $P < 0.001$ ) were severely limited on H compared to C. In experiment 1 growth was limited on M compared to C during the first 7 days of P1 ( $P < 0.01$ ) only. In experiment 2 intake ( $P < 0.001$ ) and growth ( $P < 0.001$ ) on M were limited throughout P1, compared to C but not thereafter. Therefore, in neither experiment did M cause a lower growth rate than C from 18 - 32kg. In experiment 1 there was full adaptation to M after about 10 days from 12 kg. In experiment 2 adaptation was complete by the end of the first 7 days from 18 kg. In P2 intake ( $P < 0.001$ ) and gain ( $P < 0.001$ ) were increased on HC compared to CC. By the last 7 days of P2 intake was still higher ( $P < 0.01$ ), but growth rate was no longer different to CC. Intake and gain were increased in P2 on HM compared to MM but, in general, these differences were small and not significant. In the first 7 days of P2 in Experiment 1 pigs on HM had higher intakes ( $P < 0.001$ ) and gains ( $P < 0.05$ ) than those on MM, but in experiment 2 only intake was higher ( $P < 0.01$ )

with no difference in gain. By the last 7 days of P2 there was no difference in either intake or gain between these two groups in either experiment. Pigs on HC increased intake by more than those on HM. There was, therefore, a significant interaction for food intake ( $P < 0.05$ , in Experiment 1 and  $P < 0.001$ , in Experiment 2) between prior and present food.

The unexpected failure of either M food to limit growth throughout the experimental period meant that the results of these experiments could not be used as a strong test to reject either one of the frameworks. However, the ability of the pigs to compensate on M was less than that on C. The data provide some evidence that under conditions of compensation foods such as M may be limiting. This is in closer agreement with the framework 1 that predicted that consumption of a limiting food will not increase after a period of feeding on a high bulk food (Framework 1).

## **3.2 INTRODUCTION**

Chapter 2 described two frameworks for understanding and predicting food intake. In framework 1 (Adolph, 1947; Conrad *et al.*, 1964; Black, 1984; Emmans, 1981; Mertens, 1994; Kyriazakis and Emmans, 1999), an animal is predicted to eat at a level that will allow its potential performance to be achieved, subject to its capacity to deal with some constraints, such as food bulk, not being exceeded. In recent years this framework has been criticised (e.g. Grovum, 1987; Ketelaars and Tolkamp, 1992), particularly in its application to ruminants. Framework 1 implies that an animal's ability to consume food bulk should be little affected by its physiological state or (after a period of adaptation), by previous feeding. There is, however, evidence that the intake of both medium and low quality forages is increased in ruminants in response to changes in state such as pregnancy and lactation (Weston, 1982; 1988). Evidence that the capacity of the animal to deal with such limiting foods is affected by such changes does not fit easily into Framework 1.

Framework 2 (Tolkamp and Ketelaars, 1992) does not consider food intake to be generally constrained by bulk even on foods of poor quality where growth rate is greatly reduced. The observed level of intake is seen as that which allows the animal to maximise some 'efficiency', specifically the ratio of net energy intake to oxygen consumption. From this point of view an increase in an animal's ability to consume more of poorer quality foods, as the result of a change in physiological state, can be explained in terms of such an increase leading to the maximum efficiency that can be attained in the new state on that food.

Chapter 2 compared the results of a temperature experiment on growing pigs with the predictions of the two frameworks. The results showed that intake appeared to be constrained by food bulk. The experiment described here was designed to consider another case where the frameworks would make different predictions of intake. A period of *ad libitum* feeding of a poor quality food, intended to reduce growth rate,

was used. It was expected that compensatory growth would be seen when this period was followed by a period of feeding on a food of high quality, in a similar way to that seen to occur after a period of controlled feeding (Wilson and Osbourn 1960; Cole *et al.*, 1968; Owen *et al.*, 1971). There is also evidence that, after a period of controlled feeding during which growth rate has been reduced, body lipid content is reduced (Cole *et al.*, 1968; Mersmann *et al.*, 1987; Stamataris *et al.*, 1991). When then fed *ad libitum* such pigs show a rapid increase in food intake and growth rate, and lipid stores are repleted (Stamataris *et al.*, 1991). In the current experiment a period of *ad libitum* feeding of a high bulk food was used to restrict growth. The feeding of high bulk foods has been shown to reduce body lipid content (Cole *et al.*, 1968), and hence such a period of feeding is seen as being analogous to a period of controlled feeding (e.g. Stamataris *et al.*, 1991).

The two frameworks agree that, following a period on a food of poor quality, there will be an increase in the subsequent intake of a food of high quality and compensatory growth will occur. However, the frameworks differ in their predictions when the new food is of moderate quality, but still one that gives a lower growth rate than that of a food of good quality. Framework 1 predicts that consumption of such a food will not be increased after a period of feeding on a poor quality food, and that no compensation will occur. In contrast framework 2 considers variation in intake to be the result of variation in the efficiency with which the ME of the food is utilised. It predicts that some compensation will occur whenever an animal is switched from a poor quality food to another food of improved quality, as long as the ME of the latter is utilised more efficiently. Therefore, framework 2 predicts that some compensation will occur, not only when animals fed a very poor quality food are switched to a high quality food, but also when they are switched to a moderate quality food, even if that food is limiting growth rate.

### **3.3 MATERIALS AND METHODS**

#### **3.3.1 EXPERIMENT 1**

##### *3.3.1.1 ANIMALS AND HOUSING*

Forty entire male Manor Meishan pigs (PIC Group, 50% Landrace, 25% Large White and 25% Meishan) were placed immediately after weaning at 4 weeks of age into individual pens. The average weaning weight of the pigs was 7.4 (s.d. 1.07) kg. The experimental unit consisted of two identical rooms separated by a central working area. Each room housed 20 pigs in two opposing lines of 10 individual cages, each with its own water supply and metal feeding trough. Underneath each feeding trough a metal tray was placed to collect food spillage. Each room had its own heating, lighting and ventilation system.

##### *3.3.1.2 EXPERIMENTAL FOODS*

Three foods were formulated and made into pellets of 3mm diameter. The control (C) food was intended not to limit growth rate and was based on micronised wheat. It contained 13.4 MJ digestible energy (DE) and 243g crude protein (CP) per kg fresh food. The other two foods included unmolassed sugar beet pulp (SBP) at levels of 35% (M<sub>35</sub>) or 56% (H<sub>56</sub>). M<sub>35</sub> had 12.3 MJ DE and 172g CP per kg fresh food and H<sub>56</sub> had 11.4 MJ DE and 156g CP per kg fresh food. M<sub>35</sub> and H<sub>56</sub> were supplemented with synthetic amino acids and vitamins and minerals in order to maintain similar calculated ratios of essential amino acids and vitamins and minerals to DE as the control food and were not limiting for growing pigs of the age and weight used in the experiment (Stranks *et al.*, 1988; Close, 1994). The M<sub>35</sub> and H<sub>56</sub> foods were intended to restrict the growth rate of the pigs to approximately 0.75 and 0.50 respectively of that on C. The detailed compositions and chemical analyses of the foods are given in Table 3.1.

The foods were analysed for gross energy (GE), dry matter (DM), crude protein (CP), diethyl ether extract, ash, crude fibre (CF), acid detergent (ADF; Goering and van Soest, 1970) and neutral detergent fibre (NDF; Robertson and van Soest, 1977) contents and water holding capacity (WHC). The WHC was determined by the centrifugation method as described by Tsaras *et al.* (1998) subject to one change. The test tubes were not inverted after the foods had been soaked in water. This was because, after centrifugation, the SBP food samples had not formed a solid pellet, as the C food had. Inversion of the centrifugation tubes would therefore have resulted in the samples being lost from the tubes. WHC was expressed as g water /g food DM.

### 3.3.1.3 EXPERIMENTAL DESIGN

The pigs were randomly allocated to a treatment group, a room within the experimental accommodation and to a pen within their allocated room. Prior to the start of the experiment they were given a period of time to adapt to the accommodation. This period was for the length of time that it took each pig to reach 12kg liveweight (LW), and on average lasted for 10.4 (s.d. 3.9) days. During this time the pigs were fed a commercial weaner food of high quality, with 215g CP/kg (Easiwean, BOCM Pauls Ltd), *ad libitum*. The temperature during acclimatisation was intended to be thermoneutral for pigs of this age and weight and was initially set at 25°C. The temperature was gradually reduced to 20°C by the time the first pig reached 12kg and was maintained at 20°C for the remainder of the experiment.

The experiment consisted of two experimental periods. Period 1 was from 12 - 18kg and Period 2 was from 18 - 32kg. Each pig was randomly allocated to one of four treatment groups with ten pigs in each group. In treatment group 1 the pigs received the control food (C) throughout Periods 1 and 2 (CC). In treatment group 2 the pigs received the medium food (M<sub>35</sub>) throughout Periods 1 and 2 (M<sub>35</sub>M<sub>35</sub>). In treatment

group 3 the pigs received the high bulk food ( $H_{56}$ ) in Period 1 followed by C in Period 2 ( $H_{56}C$ ). In treatment group 4 the pigs received food  $H_{56}$  in Period 1 followed by  $M_{35}$  in Period 2 ( $H_{56}M_{35}$ ).

### 3.3.1.4 MANAGEMENT AND MEASUREMENTS

The pigs were weighed daily at 9.00 h immediately prior to feeding. Food was given twice daily at 09.30 and 16.30 h, in order to minimise food spillage, with approximately half the daily allocation being given at each feeding. The pigs were fed *ad libitum* with refusals being maintained at 10 - 15% of daily intake. When the pigs were changed from  $H_{56}$  to either C or  $M_{35}$  the amount of food offered was increased to approximately twice that offered on  $H_{56}$  the previous day. This was to accommodate any large increases in intake that may have occurred following the period of feeding on H (Stamataris *et al.*, 1991). Food spillage from the trays, and refusals left in the troughs, were collected daily. They were weighed and their DM determined by oven drying at 80°C for 24hrs. DM content was then used to determine the fresh weight of the food consumed. Temperature was recorded twice a day, prior to feeding, using minimum - maximum thermometers. The data from one pig from treatment group CC was removed from the statistical analysis due to an abnormally low growth rate that was not related to feeding treatment.

### 3.3.1.5 STATISTICAL ANALYSIS

The results were analysed as a completely randomised design in Minitab (Minitab Incorporated, 1996) using a General Linear Model (GLM). For analysis of the data from Period 1 the three feeding treatments (C,  $M_{35}$  and  $H_{56}$ ) were used as a factor in the model. The data were analysed for the effects of treatment upon intake, gain and food conversion efficiency (FCE). In Period 2 the effects of the food given during both Periods were examined. The hypothesis was that pigs would be able to

compensate after a period of feeding on  $H_{56}$  when given C, but not when given  $M_{35}$ , providing that this was limiting growth. Therefore, an interaction between the foods used in Periods 1 and 2 was expected. Probability values, means and standard errors of differences were obtained from this procedure.

### 3.3.2 EXPERIMENT 2

The problem raised in Experiment 1 about the extent to which  $M_{35}$  was limiting growth (see Results and Discussion) led to a second experiment intended to correct the reasons for the failure of the first experiment to be what it was intended to be.

#### *3.3.2.1 EXPERIMENTAL FOODS*

The three foods used were C, which was the same as in Experiment 1, and two new high bulk foods based on SBP. They were formulated to contain either 50% SBP ( $M_{50}$ ) or 70% SBP ( $H_{70}$ ).  $M_{50}$  had 11.6 MJ DE and 156g CP per kg fresh food and  $H_{70}$  had 10.7 MJ DE and 128g CP per kg fresh food.  $M_{50}$  and  $H_{70}$  were designed to restrict growth to a greater extent than the foods  $M_{35}$  and  $H_{56}$  used in Experiment 1. The detailed composition and chemical analyses of the foods used in this experiment are also given in Table 3.1.

#### *3.3.2.2 EXPERIMENTAL DESIGN*

The average weaning weight of the pigs was 8.2 (s.d. 0.89) kg. On average it took each pig 9.6 (s.d. 3.6) days to reach 12kg. The temperature during this time was intended to be thermoneutral for pigs of this age and weight and, as in Experiment 1, was initially set at 25°C, which was gradually reduced to 18°C by the time the first



pig reached 12kg. The temperature was maintained at 18°C throughout the experimental period because it was thought possible that the temperature of 20°C used in Experiment 1 may have been close to being too hot for the pigs on C, especially for those expected to show a compensatory food intake.

The treatment groups were analogous to those used in Experiment 1. In treatment group 1 the pigs were fed the C food throughout (CC). In treatment group 2 the pigs received the  $M_{50}$  food throughout ( $M_{50}M_{50}$ ). In treatment group 3 the pigs were fed  $H_{70}$  in Period 1 and C in Period 2 ( $H_{70}C$ ). In treatment group 4 the pigs were fed  $H_{70}$  in Period 1 and  $M_{50}$  in Period 2 ( $H_{70}M_{50}$ ).

#### *3.3.2.3 MANAGEMENT*

During the course of the experiment two pigs, one from CC and one from  $M_{50}M_{50}$ , had to be removed from the trial due to severe health problems, neither of which was associated with feeding treatment. Their data were not included in the statistical analysis.

#### *3.3.2.4 STATISTICAL ANALYSIS*

For experiment 2 we used the same statistical analysis as for Experiment 1.

Table 3.1. The composition and chemical analyses (g/kg as fed) of the foods used in Experiments 1 and 2

	C (Exp.1 and	Food			
		35% SBP (M <sub>35</sub> )	50% SBP (M <sub>50</sub> )	56% SBP (H <sub>56</sub> )	70% SBP (H <sub>70</sub> ) (Exp.2)
<b>Ingredients</b>					
Micronised wheat	712.2	443.1	327.9	281.8	174.0
Sugar beet pulp	0.0	350	500	560	700
Fish Meal	180.0	112	82.9	71.2	44.0
Sogipro	65.0	40.4	29.9	25.7	15.9
Mineral/vitamin pre mix	12.5	12.5	12.5	12.5	12.5
Maize oil	20.0	19.6	19.5	19.5	19.3
Lysine hydrochloride	2.3	4.3	5.3	5.6	6.6
DL-methionine	0.2	1.5	2.1	2.3	2.7
L-threonine	1.3	2.3	2.7	2.8	3.1
L-tryptophan	0.0	0.5	0.7	0.8	1.1
Monosodium phosphate	6.5	13.5	16.5	17.9	20.8
Salt	0.0	0.0	0.0	0.0	0.0
Limestone	0.0	0.0	0.0	0.0	0.0
Total	1000.0	1000.0	1000.0	1000.0	1000.0
<b>Composition (g or MJ/kg fresh food)</b>					
Dry matter	889.5	895.9	883.0	895.4	875.0
Crude protein	242.7	172.0	156.3	155.7	127.7
Ether extract	44.4	36.1	31.1	30.8	26.8
Ash	69.0	80.7	85.7	83.1	80.0
Crude fibre	12.2	55.5	90.1	77.3	114.6
Acid detergent fibre	26.4	84.4	125.4	110.1	157.6 <sup>a</sup>
Neutral detergent fibre	88.3	157.7	212.9	202.3	273.8
Water holding capacity (g water/g dry	3.50	6.68	7.16	8.61	10.02
Digestible energy (MJ/kg)	13.4	12.3	11.6	11.4	10.7
Gross energy (MJ/kg)	16.4	16.0	15.7	15.8	15.3

<sup>a</sup> estimated.

## **3.4 RESULTS**

### **3.4.1 EXPERIMENT 1**

#### *3.4.1.1 PERIOD 1*

The performance of the pigs in Period 1 is given in Table 3.2. There were highly significant effects (at most  $P = 0.01$ ) of feeding treatment on food intake, gain and FCE. The difference in intake between C and  $M_{35}$  was not significant, but the pigs on  $H_{56}$  ate significantly less ( $P < 0.001$ ) than those on C. Gain on C was higher than that on either  $M_{35}$  (ns) or H ( $P < 0.001$ ). Contrary to our expectations, and the intentions of the experimental design,  $M_{35}$  could not be shown to be limiting when compared to C.

**Table 3.2. Experiment 1.** *The performance in Period 1 of pigs fed one of three foods differing in sugar beet pulp (SBP) content, 0% SBP (C), 35% SBP ( $M_{35}$ ) or 56% SBP ( $H_{56}$ ), from 12 - 18kg.*

Treatment (%SBP)	Food intake (g d <sup>-1</sup> )	Gain (g d <sup>-1</sup> )	FCE (food gain:intake)
C (0)	722	544	0.744
$M_{35}$ (35)	671	487	0.659
$H_{56}$ (56)	453	309	0.520
s.e.d	60	38	0.034
Effects			
Treatment	**	***	***

The performance of the pigs during the first and last 7 days of Period 1 is given in Table 3.3. During the first 7 days of the period there were highly significant effects of treatment on food intake and gain ( $P < 0.001$ ). Although there was no statistical difference in the intake of C and M<sub>35</sub>, the difference in the gain on these two foods was significant with that on M<sub>35</sub> being only 0.66 of that on C ( $P < 0.01$ ). M<sub>35</sub> was thus a limiting food in the first 7 days. Intake ( $P < 0.001$ ) and gain ( $P < 0.001$ ) were both severely restricted on H<sub>56</sub> compared to C. During the last 7 days of Period 1 (Table 3.3) there were no significant effects of treatment on intake but there was a significant ( $P < 0.01$ ) effect of treatment on gain. There was no difference between the gains on M<sub>35</sub> and C so that, by the end of Period 1, M<sub>35</sub> was no longer a food that was limiting gain. Gain on H<sub>56</sub> was still significantly ( $P < 0.05$ ) reduced compared to that on C.

**Table 3.3. Experiment 1.** The performance of pigs fed one of three foods differing in sugar beet pulp (SBP) content, 0% SBP (C), 35% SBP (M<sub>35</sub>) or 56% SBP (H<sub>56</sub>), during the first and last 7 days of Period 1 (12 - 18kg).

Treatment (%SBP)	Food intake (g d <sup>-1</sup> )		Gain (g d <sup>-1</sup> )		FCE (food gain:intake)	
	First 7 days	Last 7 days	First 7 days	Last 7 days	First 7 days	Last 7 days
C (0)	713	744	550	549	0.766	0.739
M <sub>35</sub> (35)	621	875	362	589	0.574	0.681
H <sub>56</sub> (56)	425	794	112	445	0.251	0.568
s.e.d.	57	57	53	42	0.062	0.051
Effects	***	ns	***	**	***	**
Treatment						

There was a highly significant effect of treatment on FCE during Period 1 ( $P < 0.001$ , Table 3.2). As the energy content of the food was reduced FCE was also reduced with the pigs on C the most, and those on  $H_{56}$  the least, efficient. Splitting the FCE data into the first and last 7 days of the period (Table 3.3) revealed that as the period progressed the pigs were able to utilise  $M_{35}$  and  $H_{56}$  more efficiently.

### 3.4.1.2 PERIOD 2

The results from the whole of Period 2 are given in Table 3.4. The pigs on  $H_{56}C$  ate  $304\text{g d}^{-1}$  ( $P < 0.001$ ) more than those on CC and thus showed a considerable compensatory intake. The pigs on  $H_{56}M_{35}$  also increased their intake compared to those on  $M_{35}M_{35}$ , but only by  $196\text{g d}^{-1}$  ( $P < 0.01$ ). The gain of the pigs on  $H_{56}C$  was  $80\text{g d}^{-1}$  ( $P < 0.05$ ) higher than on CC. But gain for the pigs on  $H_{56}M_{35}$  was increased by only  $33\text{g d}^{-1}$  (ns) compared to  $M_{35}M_{35}$ . Over Period 2 as a whole, there was thus a small compensatory gain for the pigs changed from  $H_{56}$  to C, but hardly any for those changed from  $H_{56}$  to  $M_{35}$ . The pigs on treatments  $H_{56}C$  and  $H_{56}M_{35}$  were less efficient in Period 2 than those on CC and  $M_{35}M_{35}$  respectively, although only the first of these differences was significant (Table 3.4).

The performance of the pigs in the first and last 7 days of Period 2 is given in Table 3.5. In the first 7 days the pigs on  $H_{56}C$  increased their intake by  $426\text{g d}^{-1}$  ( $P < 0.001$ ) and their growth rate by  $363\text{g d}^{-1}$  ( $P < 0.001$ ) compared to those on CC. The pigs on  $H_{56}M_{35}$  increased their intake by  $263\text{g d}^{-1}$  ( $P < 0.001$ ) and their growth rate by  $138\text{g d}^{-1}$  ( $P < 0.05$ ) compared to those on  $M_{35}M_{35}$ . The differences between these differences, in both intake and gain, were significant ( $P < 0.05$ ). Treatment in Period 1 had no effect on FCE in the first 7 days of Period 2, although the pigs on C were significantly more efficient than those on  $M_{35}$  ( $P < 0.001$ ).

In the final 7 days of Period 2 the  $H_{56}C$  pigs were eating more than the CC pigs ( $1450$  v  $1254\text{g d}^{-1}$ ;  $P < 0.01$ ). In contrast the  $H_{56}M_{35}$  pigs were eating only  $37\text{g d}^{-1}$  (ns) more

than the M<sub>35</sub>M<sub>35</sub> pigs. The growth rates on the four treatments were not significantly different. The pigs from H<sub>56</sub> were less efficient on both C and M<sub>35</sub>, than those fed these foods throughout, although the difference was significant ( $P < 0.01$ ) only for the H<sub>56</sub>C treatment.

**Table 3.4. Experiment 1.** *The effects of prior feeding on three foods differing in sugar beet pulp (SBP) content in Period 1 (0% SBP (C), 35% SBP (M<sub>35</sub>) or 56% SBP (H<sub>56</sub>)) on the subsequent performance of pigs fed one of two foods differing in SBP content (C or M<sub>35</sub>) during Period 2 (18 - 32kg).*

Food (% sugar beet pulp)		Food intake	Gain	FCE
Period1	Period 2	(g d <sup>-1</sup> )	(g d <sup>-1</sup> )	(food gain:intake)
C (0)	C (0)	1071	693	0.649
M <sub>35</sub> (35)	M <sub>35</sub> (35)	1275	748	0.590
H <sub>56</sub> (56)	C (0)	1375	773	0.563
H <sub>56</sub> (56)	M <sub>35</sub> (35)	1471	781	0.554
s.e.d		50	38	0.031
Effects				
Food in Period 1		***	*	**
Food in Period 2		***	ns	ns
Interaction		*	ns	ns

**Table 3.5. Experiment 1.** The effects of prior feeding on three foods differing in sugar beet pulp (SBP) content in Period 1 (0%SBP (C), 35% SBP (M<sub>35</sub>) or 56% SBP (H<sub>56</sub>)) on the subsequent performance of pigs during the first and last 7 days of Period 2 (18 - 32kg) where pigs were fed one of two foods differing in SBP content (C or M<sub>35</sub>)

Food (% sugar beet pulp)		Food intake (g d <sup>-1</sup> )		Gain (g d <sup>-1</sup> )		FCE (food gain:intake)	
Period1	Period 2	First 7 days	Last 7 days	First 7 days	Last 7 days	First 7 days	Last 7 days
C (0)	C (0)	870	1254	594	746	0.684	0.595
M <sub>35</sub> (35)	M <sub>35</sub> (35)	1089	1468	656	809	0.601	0.553
H <sub>56</sub> (56)	C (0)	1296	1450	957	730	0.735	0.507
H <sub>56</sub> (56)	M <sub>35</sub> (35)	1352	1505	794	749	0.595	0.500
s.e.d.		57	59	58	44	0.042	0.031
Effects							
Food in Period 1		***	*	***	ns	ns	**
Food in Period 2		***	**	ns	ns	***	ns
Interaction		*	ns	**	ns	ns	ns

### 3.4.1.3 GROWTH AND FOOD INTAKE OVER TIME

The weight by time curves of the pigs on CC and  $M_{35}M_{35}$  are shown in Figure 3.1. The time lag established during the first few days for the pigs on  $M_{35}M_{35}$  did not subsequently change. This shows that, as judged by growth rate,  $M_{35}$  was not a limiting food after the first short period of time for which it was fed.

Figure 3.2 shows the weight by time curves for the four treatment groups in Period 2. There was no difference between CC and  $M_{35}M_{35}$  although, if anything the  $M_{35}M_{35}$  pigs grew faster than the CC pigs (Table 3.4). The faster initial growth on both C and  $M_{35}$  after the feeding on  $H_{56}$  can be clearly seen, with little to choose between  $H_{56}C$  and  $H_{56}M_{35}$ .

Figure 3.3 shows the intakes of the four treatment groups in Period 2. Intake on  $M_{35}M_{35}$  was significantly higher than that on CC. From this graph the extent to which intake on  $H_{56}C$  exceeds that on CC is greater than that by which intake on  $H_{56}M_{35}$  exceeds intake on  $M_{35}M_{35}$  is clear. On the second day after the pigs were given a food of improved quality there was a drop in food intake that was probably in part a response to the high intake of the previous day. Thereafter the rate of intake of this food steadily increased over time. Although the  $M_{35}M_{35}$  pigs ate significantly more food than those on CC, there was no such difference between  $H_{56}C$  and  $H_{56}M_{35}$  as can be clearly seen from Figure 3.3. In addition the difference in the food intake of the pigs changed from  $H_{56}$  onto either C or  $M_{35}$ , compared to when C and  $M_{35}$  were fed continuously throughout, became less over time. At the beginning of Period 2 the pigs that were changed from  $H_{56}$  to C were consuming approximately 500g d<sup>-1</sup> more than those fed C throughout but, by the end of Period 2, this difference had been reduced to 200g d<sup>-1</sup>. The pigs that were changed from  $H_{56}$  to  $M_{35}$  were consuming approximately 300g d<sup>-1</sup> more than those on  $M_{35}$  throughout at the beginning of Period 2, by the end of the Period there was no real difference in the intakes of these two treatment groups.



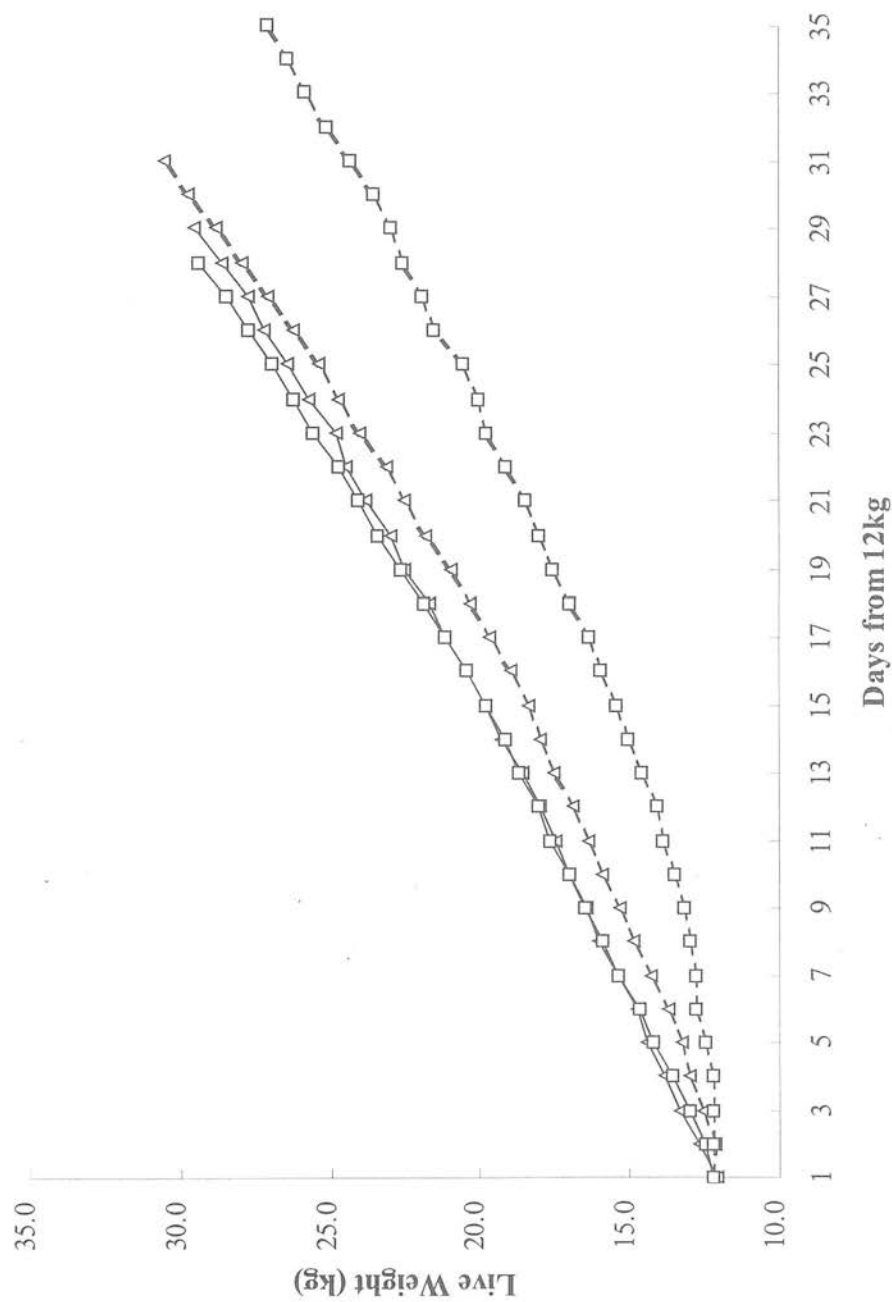
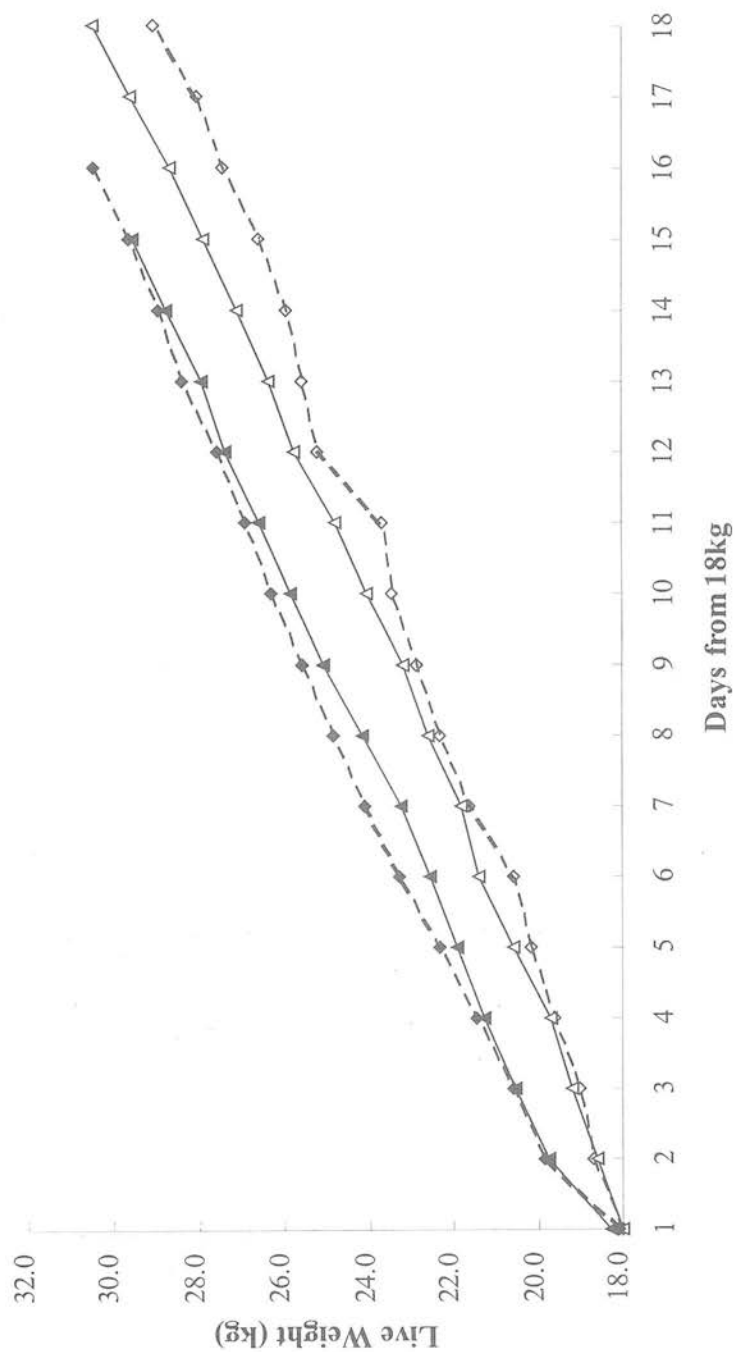


Figure 3.1. The growth curves of the pigs fed foods with 0% (C) (— $\Delta$ —, exp. 1; — $\square$ —, exp. 2), 35% (M35, --- $\Delta$ ---, exp. 1) and 50% sugar beet pulp (M50 (--- $\square$ ---, exp. 2) throughout. The graphs are continued until the day that the first pig reached 32kg.



**Figure 3.2.** Growth curves, during Period 2 (18 - 32kg) in exp. 1 by treatment. Treatment CC, fed C with 0% sugar beet pulp (SBP) throughout ---△---, treatment M35M35 fed M35 with 35% SBP throughout, ---△---, treatment H50C, fed the H50 food with 50% SBP throughout, ---◇---, and treatment H50M35 fed H50 in period 1 and M35 in period 2 ---▲---. The graphs are continued until the day that the first pig reached 32kg.

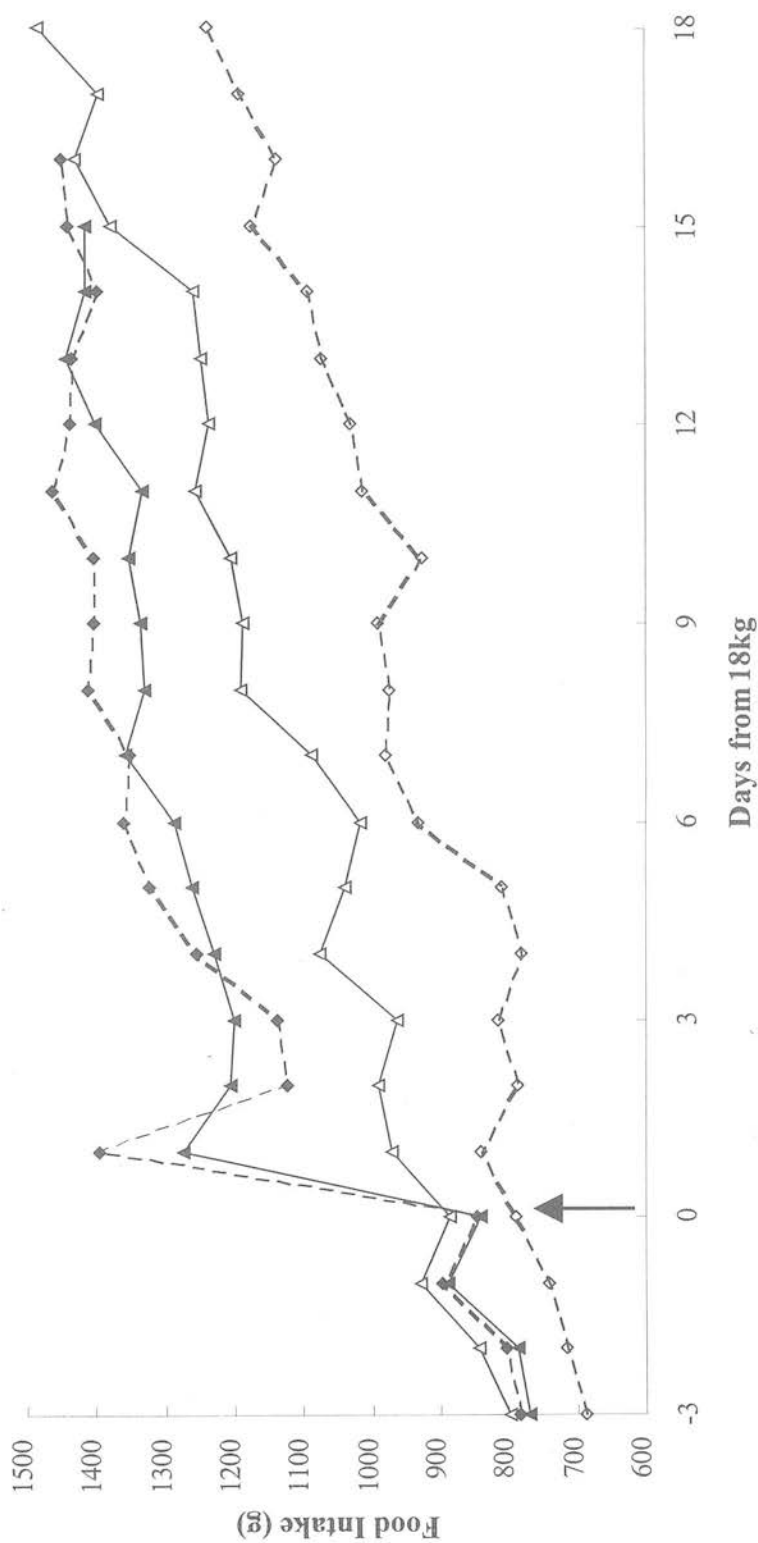


Figure 3.3. Food intake in exp 1, during Period 2 (18 - 32kg) and the last 3 days of period 1, by treatment. Treatment CC, fed C with 0% sugar beet pulp (SBP) throughout ---◇---, treatment M35M35 fed M35 with 35% SBP throughout, ---△---, treatment H50C fed the H50 food with 50% SBP in period 1 and C in period 2, --◇--, and treatment H50M35 fed H50 in period 1 and M35 in period 2 ---△---. The graphs are continued until the day that the first pig reached 32kg. The arrow denotes the point at which the foods were changed from H50 to either C or M35 (i.e. 18kg).

### 3.4.2 EXPERIMENT 2

#### 3.4.2.1 PERIOD 1

The performance of the pigs in Period 1 is given in Table 3.6. On C performance was virtually the same as that in Experiment 1 (Table 3.2, Figure 3.1). There were highly significant effects of treatment ( $P < 0.001$ ) on food intake, gain and FCE, all of which decreased as the level of inclusion of SBP increased. The rate of gain was lower on  $M_{50}$  than on C.  $M_{50}$  was thus a limiting food.

**Table 3.6. Experiment 2.** *The performance in Period 1 of pigs fed one of three foods differing in sugar beet pulp (SBP) content, 0% SBP (C), 50% SBP ( $M_{50}$ ) and 70% SBP ( $H_{70}$ ), from 12 - 18kg.*

Treatment (% SBP)	Food intake (g d <sup>-1</sup> )	Gain (g d <sup>-1</sup> )	FCE (food gain:intake)
C (0)	732	564	0.769
$M_{50}$ (50)	612	301	0.494
$H_{70}$ (70)	536	183	0.347
s.e.d	24	22	0.0315
Effects			
Treatment	***	***	***

The performance of the pigs during the first and last 7 days of Period 1 is given in Table 3.7. During the first 7 days there was a highly significant effect of treatment ( $P < 0.001$ ) on intake, gain and FCE. All decreased as the level of inclusion of SBP

increased. With gain on  $M_{50}$  being only 0.17 of that on C it was clearly a very limiting food at this time.

During the last 7 days of Period 1 the intake of  $M_{50}$  was higher than that of C ( $P < 0.05$ ) and  $H_{70}$  (ns). There was a highly significant effect of treatment ( $P < 0.001$ ) on gain, which was significantly higher ( $P < 0.01$ ) on C than that on  $M_{50}$  and  $H_{70}$ .  $M_{50}$  was thus a limiting food throughout Period 1 as intended.

**Table 3.7. Experiment 2.** The performance of pigs fed one of three foods differing in sugar beet pulp (SBP) content, 0% SBP (C), 50% SBP ( $M_{50}$ ) or 70% SBP ( $H_{70}$ ), during the first and last 7 days of Period 1 (12 - 18kg).

Treatment (%SBP)	Food intake (g d <sup>-1</sup> )		Gain (g d <sup>-1</sup> )		FCE (food gain:intake)	
	First 7 days	Last 7 days	First 7 days	Last 7 days	First 7 days	Last 7 days
C (0)	702	766	546	575	0.775	0.740
$M_{50}$ (50)	403	845	93	434	0.217	0.516
$H_{70}$ (70)	296	772	-41	336	-0.168	0.435
s.e.d.	39	38	41	52	0.012	0.059
Effects	***	ns	***	***	***	***
Treatment						

### 3.4.2.2 PERIOD 2

The performance of the pigs in Period 2 is given in Table 3.8. Growth rate on  $M_{50}$ , 683g d<sup>-1</sup>, was not significantly less than that on CC, 717 g d<sup>-1</sup>, in the whole

period, so that  $M_{50}$  could no longer be seen as a limiting food when fed continuously. The pigs on  $H_{70}C$  increased their food intake by  $412 \text{ g d}^{-1}$  ( $P < 0.001$ ), whereas those on  $H_{70}M_{50}$  increased their intake only by  $95 \text{ g d}^{-1}$  (ns). The difference between these differences was highly significant ( $P < 0.001$ ). The gain of the pigs on  $H_{70}C$  was  $152 \text{ g d}^{-1}$  higher than for those on CC ( $P < 0.001$ ), while the gain of the pigs on  $H_{70}M_{50}$  was only  $57 \text{ g d}^{-1}$  higher than on  $M_{50}M_{50}$  (ns). The difference between these differences just failed to be statistically significant ( $P = 0.056$ ). The pigs on  $H_{70}C$  were less efficient ( $P < 0.01$ ) than those on CC, despite growing faster. The pigs on  $H_{70}M_{50}$  were no less efficient than the pigs on  $M_{50}M_{50}$ .

**Table 3.8. Experiment 2.** The effects of being fed one of three foods differing in sugar beet pulp (SBP) content in Period 1 (0% SBP (C), 50% SBP ( $M_{50}$ ) or 70% SBP ( $H_{70}$ )) on the subsequent performance of pigs fed one of two foods differing in SBP content (C or  $M_{50}$ ) during Period 2 (18 - 32kg).

Food (% SBP)		Food intake (g d <sup>-1</sup> )	Gain (g d <sup>-1</sup> )	FCE (food gain:intake)
Period 1	Period 2			
C (0)	C (0)	1093	717	0.653
$M_{50}$ (50)	$M_{50}$ (50)	1359	683	0.504
$H_{70}$ (70)	C (0)	1505	869	0.579
$H_{70}$ (70)	$M_{50}$ (50)	1454	740	0.512
s.e.d		60	34	0.020
Effects				
Food Period 1		***	***	*
Food Period 2		*	**	***
Interaction		***	ns	**

The performance of the pigs in the first and last 7 days of Period 2 is given in Table 3.9. In neither of the sub-periods was growth on  $M_{50}M_{50}$  significantly less than that on CC so that  $M_{50}$  could not be seen as a limiting food when fed continuously for any part of period 2. During the first 7 days the pigs on  $H_{70}C$  increased intake and gain by more than those on  $H_{70}M_{50}$  ( $P < 0.01$ ). Pigs on  $H_{70}C$  increased their intake by  $459 \text{ gd}^{-1}$  ( $P < 0.001$ ) while those on  $H_{70}M_{50}$  increased theirs by  $185 \text{ gd}^{-1}$  ( $P < 0.01$ ). The pigs on  $H_{70}C$  increased their gain by  $349 \text{ gd}^{-1}$  ( $P < 0.001$ ), while those on  $H_{70}M_{50}$  increased theirs by  $112 \text{ gd}^{-1}$  (ns). The difference between these differences was highly significant ( $P < 0.01$ ). The only effect on FCE was that the pigs fed  $M_{50}$  were less efficient than those fed C ( $P < 0.001$ ).

During the last 7 days of Period 2 the intake of the pigs on  $H_{70}C$  was greater, by  $322 \text{ gd}^{-1}$  ( $P < 0.001$ ), than that of those on CC. The pigs on  $H_{70}M_{50}$  showed no increase at all compared to those on  $M_{50}M_{50}$ . The differences between these differences were highly significant ( $P < 0.01$ ). There were no significant differences in rate of gain between treatments with the consequence that the  $H_{70}C$  pigs were much less efficient than CC.

**Table 3.9. Experiment 2.** The effects of being fed one of three foods differing in sugar beet pulp (SBP) content in Period 1 (0% SBP (C), 50% SBP (M<sub>50</sub>) or 70% SBP (H<sub>70</sub>)) on the subsequent performance of pigs during the first and last 7 days of Period 2 (18 - 32kg) where pigs were fed one of two foods differing in SBP content (C or M<sub>50</sub>)

Food (% sugar beet pulp)		Food intake (g d <sup>-1</sup> )		Gain (g d <sup>-1</sup> )		FCE (food gain:intake)	
Period 1	Period 2	First 7 days	Last 7 days	First 7 days	Last 7 days	First 7 days	Last 7 days
C (0)	C (0)	911	1280	605	817	0.658	0.636
M <sub>50</sub> (50)	M <sub>50</sub> (50)	1080	1605	599	771	0.551	0.486
H <sub>70</sub> (70)	C (0)	1370	1602	954	793	0.698	0.499
H <sub>70</sub> (70)	M <sub>50</sub> (50)	1265	1603	711	741	0.562	0.463
s.e.d.		60	85	59	57	0.037	0.036
Effects							
Food Period 1		***	*	***	ns	ns	**
Food Period 2		ns	**	**	ns	***	***
Interaction		**	**	**	ns	ns	*



### 3.4.2.3 GROWTH AND FOOD INTAKE OVER TIME

Figure 3.1 shows the weight by time curves of the pigs fed C and  $M_{50}$  throughout the whole of the experiment. Growth rate on  $M_{50}M_{50}$  was severely restricted for the first 11 days compared to that achieved on CC. After this the growth rate on  $M_{50}$  improved so that the delay, of about 10 days, incurred by  $M_{50}$  was not increased any further compared to C.

Figure 3.4 shows the weight by time curves for the four treatments groups in period 2. There was no difference between CC and  $M_{50}M_{50}$ , although after the first 8 days growth on CC is slightly but not significantly higher than that on  $M_{50}M_{50}$  (Table 3.9). The faster initial growth on C and  $M_{50}$  after feeding on  $H_{70}$  can be seen clearly and after day 3 pigs that were changed from H to C grew significantly faster than those that were changed from  $H_{70}$  to  $M_{50}$  (Table 3.9). This pattern continued throughout Period 2. The ability of pigs on  $H_{70}C$  to increase growth by more than those on  $H_{70}M_{50}$  compared to CC and  $M_{50}M_{50}$  respectively can be seen clearly.

Figure 3.5 shows that when the pigs were changed from  $H_{70}$  to a food of improved quality there was an immediate and marked increase in intake. The extent to which the pigs that moved from  $H_{70}$  to C increased their intake, compared to those continued on C, was much greater than for those moved from  $H_{70}$  to  $M_{50}$ . At the beginning of Period 2 the  $H_{70}$  to C pigs were eating about  $500\text{g d}^{-1}$  more than the CC pigs. By the end of the period this difference had been reduced to approximately  $400\text{g d}^{-1}$ . The  $H_{70}M_{50}$  pigs ate about  $200\text{g d}^{-1}$  more than the  $M_{50}M_{50}$  pigs. By the end of the period this difference had been reduced to almost nothing.

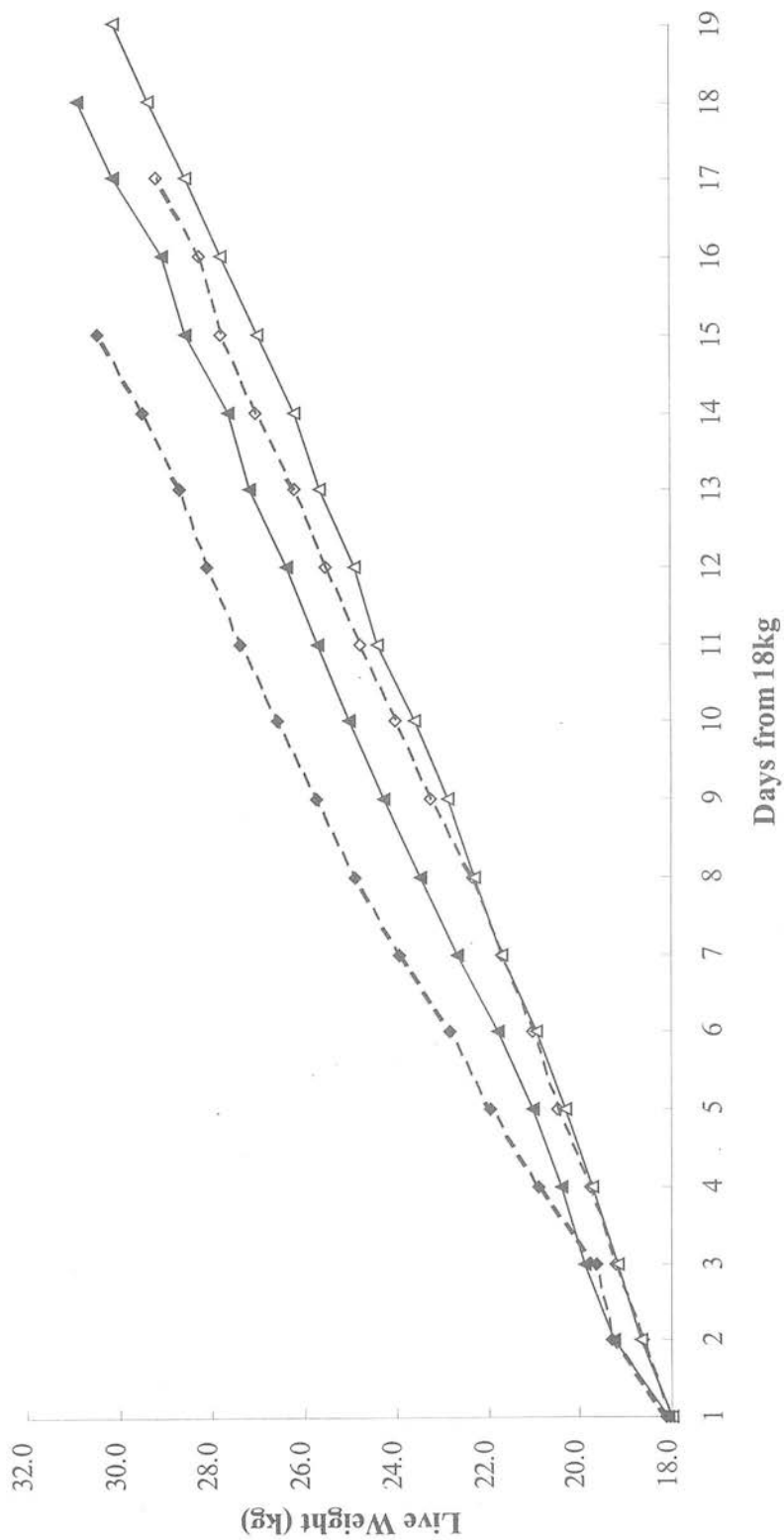


Figure 3.4. Growth curves, during Period 2 (18 - 32kg) in exp. 2 by treatment. Treatment CC, fed C with 0% sugar beet pulp (SBP) throughout ---◇---, treatment M50M50 fed M50 with 50% SBP throughout, —△—, treatment H70C fed the H70 food with 70% SBP in period 1 and C in period 2), ---◆---, and treatment H70M50 fed H70 in period 1 and M50 in period 2 —▲—. The graphs are continued until the day that the first pig reached 32kg.

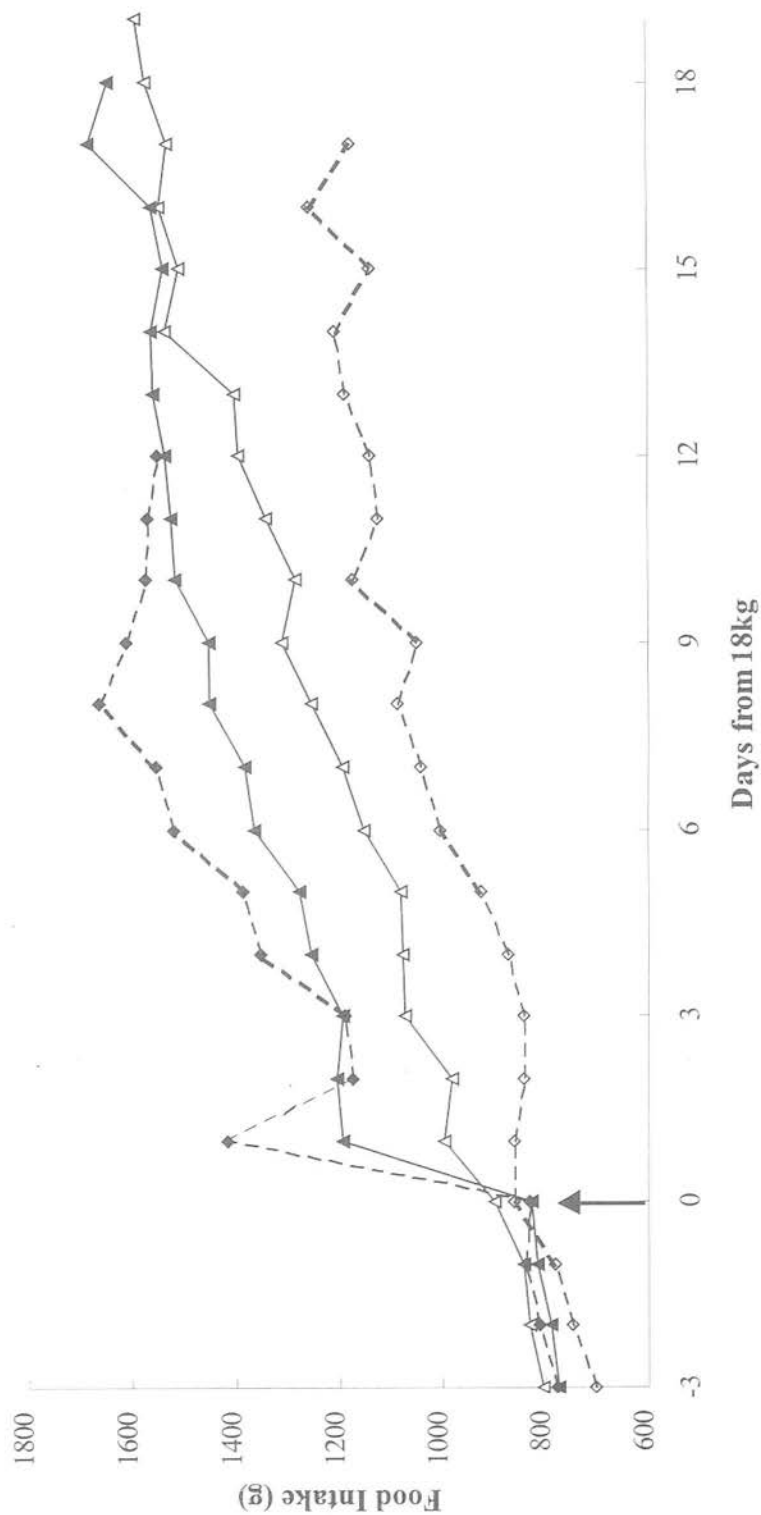


Figure 3.5. Food intake in exp. 2, during Period 2 (18 - 32kg) and the last 3 days of period 1, by treatment. Treatment CC, fed C with 0% sugar beet pulp (SBP) throughout ---◇---, treatment M50M50 fed M50 with 50% SBP throughout, ---△---, treatment H70C fed the H70 food with 70% SBP in period 1 and C in period 2, --◆--, and treatment H70M50 fed H70 in period 1 and M50 in period 2 ---▲---. The graphs are continued until the day that the first pig reached 32kg. The arrow denotes the point at which the foods were changed from H70 to either C or M50 (i.e. 18kg).

### **3.5 DISCUSSION**

The two experiments described in this paper follow an earlier one using environmental temperature as a variable (Chapter 2). They were intended to provide severe tests of the two current frameworks for the prediction and understanding of food intake, particularly in pigs. Briefly, framework 1 assumes that an animal will eat to achieve maximum performance, subject to constraints, while framework 2 assumes that an animal will eat to achieve maximum biological efficiency. Efficiency is defined as the ratio of net energy eaten to the amount of oxygen consumed, and it is asserted that this has a maximum value at a particular level of intake of a given food. Framework 1 has been criticised for ruminants by Grovum (1987), Ketelaars and Tolkamp (1992) and Tolkamp (1999); framework 2, in turn, has been criticised by Emmans and Kyriazakis (1995b) and Forbes (1995).

In the context of the current experiments both frameworks predicted that the intake of a high quality food, such as C, would increase following the feeding of a food that severely limited growth rate, such as H<sub>56</sub> and H<sub>70</sub>. However, they differed in their predictions of the intake of a food of moderate, but still limiting, quality (such as the M<sub>35</sub> and M<sub>50</sub> used here were intended to be) after a period of feeding on a severely limiting food. Framework 1 predicted no increase in intake compared to that seen when the moderately limiting food was fed continuously, while framework 2 predicted that intake would be increased.

In view of the results of the experiments, and the consequences of these for the intended design, the discussion will be in two parts. In the first we will see the results against the background of the theoretical frameworks described in the Introduction, and briefly above. In the second they will be discussed for their relevance to questions of compensatory growth and efficiency.

### 3.5.1 INTAKE THEORIES

The design of both experiments called for foods that would limit growth to a lesser ( $M_{35}$  and  $M_{50}$ ) and to a greater extent ( $H_{56}$  and  $H_{70}$ ) compared to a control food C. The results of the first experiment (in which  $M_{35}$  was not a limiting food throughout period 1) led us to increase the SBP content of  $M_{35}$  to give  $M_{50}$ , and of  $H_{56}$  to give  $H_{70}$ . While  $H_{56}$  (56%SBP) and  $H_{70}$  (70%SBP) both caused severe reductions in growth between 12 and 18 kg the effects of  $M_{35}$  (35% SBP) and  $M_{50}$  (50%SBP) were not those that the design called for (Tables 3.3 and 3.7).  $M_{35}$  did limit growth in the first week from 12 kg but it was no longer limiting in the week leading up to 18 kg and thereafter.  $M_{50}$  was limiting for the whole of the first period from 12 to 18 kg as intended, but not thereafter (Table 3.8). Previous work by Tsaras *et al.* (1998) on growing pigs, and by Brouns *et al.*, (1995), Verstergaard and Danielsen (1998) and Whittaker *et al.*, (2000) on pregnant sows, led us to expect that foods containing 35% and, certainly, 50% sugar beet pulp would reduce growth rate up to at least 32kg liveweight. What we found was that our pigs were adapted fully to these foods at weights that were much lower than we had expected. Adaptation to poor quality foods has been noted before and is generally attributed to the increasing ability of the gastrointestinal tract to deal with such foods over time (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). Adaptation occurs through the enlargement of some of the sections of the gastrointestinal tract (Low, 1985; Kyriazakis and Emmans, 1995). Despite such adaptation pigs on both  $H_{56}$  and  $H_{70}$  were unable to increase their intake sufficiently to allow growth rate up to 18kg liveweight to be maintained. Tsaras *et al.* (1998) found that after 7 days from 12kg liveweight pigs given a food with 32% SBP grew at only 0.80 of the rate shown by control pigs. Whittaker *et al.* (2000) found that first parity pregnant sows of about 180kg ate only 2.6kg/day of a food with 60% SBP, whilst Brouns *et al.*, (1995) found that dry sows in late gestation and weighing 232kg, ate only 4.0kg/day of a food with 50% SBP. On the basis of these results, the high consumption levels of our pigs on foods with 35% and 50% SBP and the excellent growth rates obtained were unexpected.

If it were to be the case that growth rate on the control food C was reduced then it would be possible that this reduced rate could be attained on a food with a high SBP content. But, on the foods of high quality, the growth rates obtained by Tsaras *et al.* (1998) were virtually identical to ours, when assessed over the same range in liveweight. Another possible reason for the high consumption of the 35% and 50% SBP foods is that our pigs were 25% Meishan, while those of Tsaras *et al.* (1998) were not. But, in our earlier experiment (Chapter 2) the proportion of the Meishan breed in the pigs did not affect the intake of a food with 65% SBP. So we cannot account for the difference either because of a difference in the absolute level of performance, or the small difference in breed composition.

An important requirement of the test was that the food of moderate quality would limit the performance of growing pigs throughout the whole of the experiment. In Experiment 1 we did not manage to achieve this as the  $M_{35}$  food did not restrict growth rate even for the week leading up to 18 kg. In experiment 2 we increased the SBP content of the M food to try to produce the necessary effects. But food  $M_{50}$  used in the second experiment was not a food that limited growth rate throughout the whole of the experiment either. As neither  $M_{35}$  nor  $M_{50}$  was a limiting food throughout, the experiments cannot be seen as the critical tests of the intake frameworks that they were intended to be. However, in both experiments there was a significant interaction for food intake in Period 2. The pigs changed from H to C were able to increase their intake by more than the pigs that were changed from H to M. In the first 7 days of period 2 the H to M pigs did not compensate in gain as much as did the H to C pigs. According to Framework 1 the reduced ability to compensate on a food of moderate quality suggests that food intake on such a food was constrained by the pigs' capacity to consume food bulk in relation to gut capacity. According to Framework 2 a food of moderate quality was expected to be a less efficient food than C, and so the degree to which compensation could occur on such a food would be less than that occurring on C. We are, therefore, unable to reject either of the theories based on the results we see here.

Although the two experiments cannot be used to reject either one of the frameworks they do provide some indirect evidence in favour of framework 1. In both experiments in the last 7 days of period 2 pigs that were changed from H to C showed substantially higher intakes than the pigs that were on C throughout. The absence of an improvement in gain at this time may be explained if the pigs were laying down an increased amount of lipid (see below). However, during the same time period there is no difference in either the intake or gain of the pigs that were changed from H to M compared to the pigs that were fed M throughout.

From the viewpoint of framework 1 the pigs that were fed C throughout were assumed to be achieving their potential performance, i.e. to be achieving their desired protein and lipid deposition rates (Kyriazakis and Emmans, 1999). In the last 7 days of Period 2, therefore, the fact that the pigs changed from H to C were still compensating, could be taken as evidence that at this time they had not achieved their desired body composition (Kyriazakis *et al.*, 1991) and hence showed a need for continuing compensation. The fact that the pigs that were changed from H to M did not continue to show an improved intake in the last 7 days of Period 2 suggests that, under conditions where compensation was possible, M became a limiting food. The pigs were apparently unable to increase their intake of M by enough to allow compensation to continue.

In contrast to the prediction of framework 1, framework 2 predicted that similar compensatory intake would occur if pigs were switched from a low quality food to one of two better quality foods, the energy of which were to be used with similar high efficiency. If the similar performance of the MM and the CC pigs at the end of period 2 reflected a similar efficiency of utilisation of C and M, then a lower compensatory intake of M compared to C would not be expected. The observations seem, therefore, closer to predictions of framework 1 than to those of framework 2.

### 3.5.2 COMPENSATION

The effect of a period of controlled feeding upon the subsequent intake of a high quality food has been well documented (e.g. Wilson and Osbourn, 1960; Cole *et al.*, 1968; Mersmann *et al.*, 1987; Owen *et al.*, 1971; Stamataris *et al.*, 1991). After a period of controlled feeding both intake and growth rate increased where the subsequent food was of high quality. In our experiments growth rate was reduced by giving *ad libitum* access to a food of poor quality which was high in bulk, rather than by restricting the intake of a high quality food. Our results of higher growth rates and intakes on subsequent feeding of a high quality food were in agreement with this previous work. They show that a period of feeding on a high bulk food caused subsequent compensatory gains, analogous to those achieved following a period of controlled feeding when the subsequent food is one of high quality.

Compensatory growth, in a formal sense, can come about either from an increased food intake at the same FCE, or from an increased FCE at the same intake, or from a combination of these two effects. In previous experiments (Cole *et al.*, 1968; Owen *et al.*, 1971; Mersmann *et al.*, 1987; Stamataris *et al.*, 1991) compensation was achieved mainly through an increased food intake. In both of our experiments the pigs changed from H<sub>56</sub> or H<sub>70</sub> to C showed increases in intake which were substantial and persisted for the whole of Period 2 (Figures 3.3 and 3.5), although the proportional size of the increase decreased with time. In the first 7 days of period 2 intakes on H<sub>56</sub>C and H<sub>70</sub>C were 1.49 and 1.50 of those on CC, while in the last 7 days these ratios had decreased to 1.16 and 1.25 respectively. However, the increase in the rate of liveweight gain was of much shorter duration and was present only in the initial 7 days following the change in food quality (Tables 3.5 and 3.9). The decrease in the compensatory growth response with time is consistent with the results of Robinson (1964) and Owen *et al.*, (1971). The continuing higher intakes on H<sub>56</sub>C and H<sub>70</sub>C compared to CC, in conjunction with the more rapid extinction of the compensatory rate of gain, led to a marked reduction in FCE in the final 7 days of Period 2 for the compensating animals. A possible explanation, from the viewpoint



of framework 1, is that the pigs changed from H<sub>56</sub>, or H<sub>70</sub>, to C were laying down gain with a higher lipid content than those fed C throughout. This was evident in the final 7 days of Period 2, as it could have been masked by an increased gut fill, and hence liveweight gain in the first 7 days of Period 2. It has been found that during a period of controlled feeding the lipid content of gain is less than on *ad libitum* feeding (Cole *et al.*, 1968; Mersmann *et al.*, 1987; Stamataris *et al.*, 1991). The subsequent gain during compensation may have a higher lipid content (Stamataris *et al.* 1991), which would lead to a reduced FCE as was observed here (Tables 3.5 and 3.9).

Compensation on the foods of moderate quality (M<sub>35</sub> and M<sub>50</sub>), obvious only during the first 7 days of Period 2, was less than that seen on C and it was not accompanied by any reduction in FCE. From the viewpoint of framework 1 it is the poorer quality of M<sub>35</sub> and M<sub>50</sub> that limited the ability of the pigs to eat enough to compensate as fully as on C. It may also have prevented any increase in the lipid content of the gain with the consequence of no change in FCE as was observed. The suggestions about changes in the lipid content of the gain could not be tested directly, as no animals were slaughtered. Slaughter data would provide valuable information on the composition of the pigs.

### **3.6 CONCLUSIONS**

Neither of the experiments presented in this paper was exactly as it had been intended to be. Although both the moderate quality foods were expected to limit the performance for growing pigs during the weight range of 12 - 32kg, neither food did. The reasons why the pigs were able to perform so well on these foods are not clear and deserve further investigation. The results from these experiments cannot be used to reject either of the two intake frameworks. However, the data do provide some evidence, that under conditions of compensation, a food such as M may become limiting. This evidence is in closer agreement with framework 1 than framework 2.

# **CHAPTER 4**

**The short term feeding behaviour of  
growing pigs fed foods differing in  
bulk content.**

## **4.1 ABSTRACT**

We investigated the effects of foods of different bulk on the short term feeding behaviour (STFB) of sixteen individually housed pigs. The three foods used had different bulks (low - control (C), medium - 70% wheat bran (WB), and high - 70% sugar beet pulp (SBP)). We expected the different intakes of the foods to be reflected in differences in STFB. Three hypotheses were developed based on ideas about the way in which a physical constraint to intake could arise.  $H_1$ : there would be less diurnal variation in feeding on high bulk foods that limit food intake.  $H_2$ : feeding patterns on the bulky foods would be less flexible than those on C.  $H_3$ : a change in food type would result in food intake and STFB being rapidly altered to become appropriate to the new food.

There were significant differences in food intake and STFB between the foods as intended. Pigs fed WB and SBP spent longer eating and had a slower feeding rate than pigs fed C.  $H_1$  was rejected, as there was no difference in diurnal variation in intake between the foods. Feeding was not extended into the night on WB and SBP and the proportion of feeding that occurred during the night was the same for all three foods.  $H_2$  was supported, as pigs fed WB and SBP were unable to maintain food intake and performance when time of access to the feeder was reduced. There was no adaptive change in STFB.  $H_3$  was supported as a change from WB or SBP to C, or vice versa, caused a rapid change in STFB so that it became appropriate to the new food. It is concluded that physical constraints to food intake, caused by food bulk, may bring about changes in STFB and that they are important for the regulation of intake of such foods.

## **4.2 INTRODUCTION**

Current theories of food intake regulation are predominantly based on the assumption that an animal will eat an amount such that its genetic potential will be achieved, subject to its capacities to deal with constraints, such as food bulk, not being exceeded (e.g. Kyriazakis and Emmans, 1999). This view has been strongly criticised (Grosvum, 1987; Ketelaars and Tolkamp, 1992; Tolkamp, 1999) so that currently there is no general agreement about the control of intake on high bulk foods.

The physiological regulation of food intake can be viewed as a system using feedback (Bray and York, 1998) with the elements including afferent signals and a controller that senses them. Some of the details of the way in which the system works are known but the operation of the whole remains obscure. It was concluded (Bethoud, 2000) that: "Behaviours such as searching for and selection and ingestion of food can ultimately only be expressed through specific actions of the nervous system. Almost a century of intense research has, however, been unable to identify clearly the neural substrate subserving these behavioural functions."

The study of STFB can help in understanding the physiological control of intake (Forbes, 1985). In a purely formal sense, daily intake is the product of the number of visits to the feeder in a day and the average intake per visit (Bigelow and Houpt, 1988; de Haer and de Vries, 1993). Hence, changes in intake must reflect changes in visit number, visit size, or both. Information on the effects of diet composition, particularly food bulk, on STFB, may help in understanding the control of food intake.

The experiment reported here was designed to study the effect of food bulk on the STFB of pigs. It was expected, from previous work (Chapter 2; Chapter 3), that there would be effects on both daily intake and in STFB. Literature reporting the effect of

food bulk on STFB is scarce. The available literature (e.g. Davies, 1977; Savory, 1980; Johnson *et al.*, 1986; Ramonet *et al.*, 1999; Savory, 1999) did not allow precise predictions to be made on the effects of food bulk on the STFB of pigs, but it was possible to develop three hypotheses for STFB. H1 is that pigs fed a high bulk food that limits intake will show less diurnal variation in their feeding. If there is a bulk constraint to food intake (e.g. Kyriazakis and Emmans, 1999; Mraz *et al.*, 1957; Tsaras *et al.*, 1998), then pigs fed foods with a high bulk content would be expected to feed more frequently, with less variable intervals, throughout the day, and perhaps even to extend their feeding into the night. H2 is that STFB would be less flexible on foods with a high bulk content. A prediction is that, when feeding time is limited by reducing time of access to the feeder, pigs fed a high bulk food will not alter STFB in a way that allows the restriction imposed to be overcome, whereas those on a food low in bulk content will. H3 is that when the composition of the food offered is changed intake, and hence STFB, will change rapidly to become appropriate to the new food.

## **4.3 MATERIALS AND METHODS**

### **4.3.1 ANIMALS AND HOUSING**

Sixteen entire male hybrid pigs (PIC Group, UK), were individually penned (mean weight 14.3, s.d. 1.09, kg). The pens were in two opposing ranks of 8 in a single room with controlled temperature and ventilation. Each pen measured 2 x 1 m with a bowl drinker at the front and a computerised feeder at the back. Each pig had minimal physical and visual contact with the pig in the adjacent pens, but had full visual contact with the pig opposite. The floors were of insulated concrete with straw. The temperature, intended to be thermoneutral (Whittemore, 1998), was 19.5 (s.d. 1.7) °C.

### **4.3.2 FOODS AND FOOD INTAKE RECORDING**

Three foods were fed as pellets. The control (C), based on micronised wheat, contained 13.2 MJ digestible energy (DE) and 243g crude protein (CP) per kg fresh food. It was expected that C would allow the genetic potential to be met. The foods of high bulk content were SBP with 70% sugar beet pulp (11.1 MJ DE and 206g CP/kg fresh) and WB with 70% wheatbran (10.0 MJ DE and 184g CP/kg fresh). SBP and WB were supplemented with synthetic amino acids, vitamins and minerals to give similar calculated ratios of protein, essential amino acids, vitamins and minerals to DE as those of C. The foods were analysed for gross energy (GE), dry matter content (DM), crude protein (CP), diethyl ether extract, ash, crude fibre (CF), acid detergent fibre (ADF; Goering and Van Soest, 1970) and neutral detergent fibre (NDF; Robertson and Van Soest, 1977) contents and for water-holding capacity (WHC, Tsaras *et al.*, 1998). The chemical composition and analyses of the foods are given in Table 4.1. SBP was formulated to limit both food intake and performance.

WB, with a moderate bulk content, was expected to be less limiting than SBP and to have a higher intake than both C and SBP (Chapter 2).

Each pen had an individual computerised feeder that contained a trough suspended on a loadcell (Morgan *et al.*, 2000a). Access was via a top hinged door that operated a microswitch when opened and closed. Each feeder was linked to a control box that contained the Feed Intake Recording Equipment (FIRE) system developed by Hunday Electronics Ltd (Newcastle - Upon - Tyne). Times of entry to, and exit from, the feeder were recorded for each visit. The duration of each visit, the number of visits per day and the interval between each visit were calculated. At 08:30 hrs the weight of the trough was recorded and a known weight of fresh food added to it. Daily intake was calculated as the difference between the weight of the trough and the weight of fresh food added, and the weight of the trough on the next morning. Pigs were fed *ad libitum*.



**Table 4.1.** *The composition and chemical analyses (g/kg as fed) of the three experimental foods: control (C), wheatbran (WB) and sugar beet pulp (SBP) foods.*

	Food		
	C	WB	SBP
<b>Ingredients (kg/tonne)</b>			
Micronised wheat	712.2	162.8	61.9
Sugar beet pulp	0.0	0.0	700.0
Wheatbran	0.0	700.0	0.0
Fishmeal	180.0	79.4	192.4
Sogipro <sup>†</sup>	65.0	14.9	5.6
Mineral/vitamin premix	12.5	12.4	12.4
Maize oil	20.0	19.9	19.8
Lysine hydrochloride	2.3	4.0	0.2
DL-methionine	0.2	0.7	0.02
L-threonine	1.3	1.2	0.1
L-tryptophan	0.0	0.0	0.3
Monosodium phosphate	6.5	1.5	7.2
Salt	0.0	1.6	0.0
Limestone	0.0	1.6	0.0
Total	1000.0	1000.0	1000.0
<b>Composition (g or MJ/kg fresh food)</b>			
Dry matter	878.6	870.4	873.4
Crude protein	242.6	183.6	206.0
Ether extract	33.3	42.5	20.2
Ash	56.0	67.0	92.0
Crude fibre	19.3	95.7	121.3
Acid detergent fibre	31.4	114.8	151.9
Neutral detergent fibre	95.8	333.2	272.4
Water-holding capacity (g water per g dry food)	3.50	4.60	10.02
Digestible energy (MJ/kg)*	13.2	10.0	11.1
Gross energy (MJ/kg)	16.6	17.1	15.3

<sup>†</sup> A protein supplement prepared from extracted soya beans with a CP of 700g/kg

\* Calculated according to book values for ingredients

### 4.3.3 EXPERIMENTAL DESIGN

Pigs were randomly allocated to a treatment and a pen. The first 5 days, on a high quality commercial food containing 195 g CP per kg (Growercare Sovereign Pellets, BOCM Pauls Ltd, Ipswich) *ad libitum*, allowed adaptation to the accommodation and the feeders. There were four experimental periods and six treatment groups (Table 4.2). Periods 1 and 2 lasted for 21 days each. Pigs were changed from C to either WB or SBP (treatments 1 and 2), from WB to either C or SBP (treatments 3 and 4) or from SBP to either C or WB (treatments 5 and 6). Adaptation for 7 days to the new food (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998) was followed by a 14 day recording period. The number of feeders available determined the number of pigs on each treatment. The change-over design in Periods 1 and 2 allowed the power of the experiment to be increased somewhat although there were still only few replicates. There were four replicates on C and six on each of WB and SBP. During Period 3 the pigs remained on the same food as that in Period 2 but they were given access to food only from 10:00 to 16:00 h. An access period of 6 h was expected to impose a degree of restriction on all of the foods, but to allow the pigs fed WB and SBP to maintain a positive weight gain. In Period 4 the pigs continued on the same food but were returned to 24 h access. By Period 3 it was expected that the pigs would be fully adapted to WB and SBP (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998; Chapter 2: Chapter 3), and 10 days for each of Periods 3 and 4 was considered to be long enough to allow adapted intake and gain to be measured. In Periods 3 and 4 there were four replicates on C and six on each of WB and SBP.

**Table 4.2.** *Design of experiment for Periods 1, 2, 3, and 4. C is the control food, WB the wheatbran-based food and SBP the sugar beet pulp-based food.*

Treatment	N	Period 1 (21 days)	Period 2 (21 days)	Period 3 (10 days)	Period 4 (10 days)
		24 hrs access	24 hrs access	6 hrs access	24 hrs access
1	2	C	WB	WB	WB
2	2	C	SBP	SBP	SBP
3	2	WB	C	C	C
4	4	WB	SBP	SBP	SBP
5	2	SBP	C	C	C
6	4	SBP	WB	WB	WB

#### **4.3.4 MANAGEMENT AND MEASUREMENTS**

The pigs were weighed, after fresh food had been added to the feeders, twice a week. Data from the FIRE feeders were downloaded daily. Every second day the pens were cleaned out and fresh straw was added. Temperature was recorded twice a day. In Periods 2 - 4 refusals were removed daily, weighed and DM determined by oven drying at 80°C for 24 h. DM was then used to determine the fresh weight of the food eaten. The feeders were calibrated for weight at the beginning of the experiment and then again at the end of Periods 1 and 2. Lights were on from 06:00 to 18:00 h.

#### **4.3.5 STATISTICAL ANALYSIS**

Intake and gain (LWG) were scaled directly to liveweight to allow for differences in weight between periods and treatments (Kyriazakis and Emmans, 1995; Chapter 2). Data from the FIRE feeders were processed in Minitab (Minitab Incorporated, 1992) to produce, for each pig day, the number of visits made to the feeder, the median visit duration and the total time spent in visits. Feeding rate (FR) was defined as food intake in a day divided by the total time spent in the feeder. Food intake per visit was

defined as intake divided by the number of visits in that day. The data were used to calculate the intervals between visits. For most pigs on most days the frequency distribution of visit duration was a negative exponential as seen in other species (Tolkamp *et al.*, 2000). In general the log of cumulative visits was linearly related to visit duration. However, for some pigs on some days a few visits were recorded as being of extremely long duration, which were clearly not part of the distribution describing the rest. These abnormally long visits were attributed to the door of the feeder sticking and failing to close after a pig had left. The entire days in which such a long visit was observed accounted for 12% of the total number of days in the experiment; these were removed from the data set. There were thus no such long visit durations in the data analysed.

The initial variables analysed were: the number of visits per day, the median visit duration, the time spent in the feeder, FR, intake per visit and intake per day. The scaled food intake (SFI, g kg<sup>-1</sup> day<sup>-1</sup>), liveweight gain and scaled liveweight gain (SLWG, g kg<sup>-1</sup> day<sup>-1</sup>) were also calculated. Variables were analysed in Genstat (Lawes Agricultural trust, 1993) using ANOVA. For all periods the random model fitted terms for individual pigs nested within time (week/day for Periods 1 and 2, or period for comparing Periods 2, 3 and 4); the fixed factor was food. In Period 2 the data were analysed with treatment as the factor. The results from Period 3 with 6 h access were compared with the average of Periods 2 and 4 with 24 h access to allow for the increase in pig size with time.

The model (Yeates *et al.*, 2001) used to analyse the data on intervals assumed two Gaussian and one Weibull distribution:

$$y = p(1/(\sigma_1\sqrt{2\pi}))\exp(-(t-\mu_1)^2/2\sigma_1^2) + \\ q(1/(\sigma_2\sqrt{2\pi}))\exp(-(t-\mu_2)^2/2\sigma_2^2) + \\ (1-p-q)(ct^{c-1}/\alpha_3^c)\exp(-(t/\alpha_3)^c)$$

where  $t = \log_e(\text{interval length in seconds})$ ;  $\sigma_1$  and  $\sigma_2$  = standard deviations of the Gaussian distributions (first and second distributions);  $\mu_1$  and  $\mu_2$  = means of the

Gaussian distributions;  $c$  = shape parameter of the Weibull distribution;  $\alpha$  = scale parameter of the Weibull distribution;  $p$  = the proportion of intervals in the first Gaussian distribution;  $q$  = the proportion of intervals in the second Gaussian distribution.

The first distribution is assumed to be of the intervals within meals, the middle one to be of intervals within meals during which animals visit the drinker and the third to be of the intervals between meals (Tolkamp and Kyriazakis, 1999; Morgan *et al.*, 2000a). The above model was fitted to the data for each pig in each period. It was expected that there would be differences in drinking between the three foods. Observations from previous experiments (Chapter 2; Chapter 3) suggested that pigs fed high bulk foods may interrupt feeding more often to drink than pigs fed a low bulk food. Differences in the size of the intermediate distribution (as a proportion of the total number of short intervals) were compared between the three foods as indications of differences in drinking behaviour.

Day and night data were separated according to (Morgan *et al.*, 200b). Examination of intervals showed that the “day” could be defined as 06:00 to 17:59 h and that the “night” could be defined as 18:00 to 05:59 h, which coincided with light and dark.

## **4.4 RESULTS**

### **4.4.1 EFFECTS OF FOOD ON PERFORMANCE AND STFB IN PERIOD 1**

Results for Period 1 are in Table 4.3. There was no difference in food intake between WB and C but both absolute and scaled food intakes were significantly less on SBP than on C ( $P < 0.001$ ). LWG on WB was 0.80 ( $P < 0.001$ ) and on SBP 0.36 ( $P < 0.001$ ) of that on C. As intended, both WB and SBP were limiting growth.

The STFB in Period 1 is in Table 4.3. Food did not affect the average number of daily visits to the feeder. WB and SBP did not differ in median visit duration, number of visits or total daily visit duration, but intake per visit and FR were greater on WB ( $P < 0.01$ ). On WB and SBP median visit duration ( $P < 0.05$ ) and total daily feeding time ( $P < 0.001$ ) were greater than on C. Intake per visit was significantly less on SBP than on either C or WB ( $P < 0.01$ ). FR on WB was 0.42 ( $P < 0.001$ ), and on SBP was 0.23 ( $P < 0.001$ ) of that on C.

### **4.4.2 EFFECTS OF FOOD ON PERFORMANCE AND STFB IN PERIOD 2**

LWG on SBP, but not on WB, was lower than on C ( $P < 0.01$ ) so that only SBP was still a limiting food.

The STFB results for Period 2 are in Table 4.4. On WB there were more visits ( $P < 0.01$ ), and a higher FR ( $P < 0.05$ ), than on SBP. Compared to C, SBP had a similar number of visits, a greater feeding time ( $P < 0.01$ ) a lower intake per visit ( $P < 0.05$ ) and a lower FR ( $P < 0.001$ ). On WB there were more visits ( $P < 0.001$ ) and a lower FR ( $P < 0.05$ ) than on C.

**Table 4. 3.** Results in Period 1 (21 days). The daily rate of absolute food intake (FI), scaled food intake (SFI), live-weight gain (LWG), scaled live-weight gain (SLWG), food conversion efficiency (FCE), median visit duration, number of visits made in a day, total visit duration and feeding rate (FR) of pigs given one of three foods differing in bulk content. The low bulk food is C, the wheatbran-based food is WB and the sugar beet pulp-based food is SBP.

Food	FI (g day <sup>-1</sup> )	SFI (g kg <sup>-1</sup> day <sup>-1</sup> )	LWG (g day <sup>-1</sup> )	SLWG (g kg <sup>-1</sup> day <sup>-1</sup> )	FCE (gain:intake)	Median visit duration (secs)	Visits/day	Total visit duration (min day <sup>-1</sup> )	Intake/ Visit (g)	FR (g min <sup>-1</sup> )
C	1321	49.5	906	32.8	0.687	24.0	89.0	51.2	15.6	26.0
WB	1364	52.2	727	27.6	0.523	51.0	95.0	125.0	15.3	11.0
SBP	755	35.1	328	15.2	0.442	53.0	93.0	129.7	8.3	6.0
s.e.d.	94.1	4.07	44.2	1.90	0.027	11.0	14.5	12.9	2.10	1.30
Significance	***	***	***	***	***	*	ns	***	**	***

**Table 4.4.** Results in Period 2 (21 days). The daily rate of absolute food intake (FI), scaled food intake (SFI), live-weight gain (LWG), scaled live-weight gain (SLWG), food conversion efficiency (FCE), median visit duration, number of visits made in a day, total visit duration and feeding rate (FR) of pigs given one of three food differing in bulk content. The low bulk food is C, the wheat bran-based food is WB and the sugar beet pulp-based food is SBP.

Food	FI (g day <sup>-1</sup> )	SFI (g kg <sup>-1</sup> day <sup>-1</sup> )	LWG (g day <sup>-1</sup> )	SLWG (g kg <sup>-1</sup> day <sup>-1</sup> )	FCE (gain:intake)	Median visit duration (secs)	Visits/ day	Total visit duration (min day <sup>-1</sup> )	Intake/ Visit (g)	FR (g min <sup>-1</sup> )
C	2004	51.2	994	24.6	0.499	36.0	86.0	65.3	30.0	32.0
WB	2165	57.9	922	24.3	0.435	27.0	173.0	96.0	13.0	23.0
SBP	1487	35.0	721	17.2	0.497	48.0	98.0	124.1	16.0	13.0
s.e.d.	245.3	7.3	76.4	2.20	0.045	13.4	23.8	16.7	6.0	4.0
Significance	*	*	**	**	ns	ns	**	*	*	***



#### 4.4.3 EFFECTS OF TREATMENT ON PERFORMANCE AND STFB IN PERIOD 2

The effect of treatment (see Table 4.2 and Materials and methods) in Period 2 are in Table 4.5. The type of bulky food fed in Period 1 had no effect on either performance or the STFB of pigs fed C in Period 2. There were no significant differences in absolute food intake, SFI, LWG SLWG, FCE or any of the visit characteristics of pigs that were changed from either WB to C or SBP to C. However, pigs that had had prior experience of WB had a feeding rate that was 1.46 that of pigs that had had prior experience of SBP ( $P < 0.05$ ).

Pigs changed to WB from SBP had a higher food intake ( $P < 0.05$ ), SFI ( $P < 0.001$ ) and SLWG ( $P < 0.05$ ) than pigs from C. Prior experience of a bulky food improved the ability to cope with SBP. The pigs changed to SBP from WB had an absolute intake 1.41 times higher and an SFI 1.40 times higher, than pigs that were changed from C. Although large, neither of these differences was statistically significant. Despite this, pigs that were changed to SBP from WB had a LWG that was significantly higher than pigs that were changed from C ( $P < 0.05$ ). The difference in SLWG between the two groups just failed to be statistically significant at  $P = 0.07$ . Pigs changed to SBP from WB had median visit duration, and total daily visit duration, that were significantly longer ( $P < 0.05$  and  $P < 0.01$  respectively) than pigs that were changed from C to SBP.

**Table 4. 5.** Results in Period 2 (21 days). The effects of feeding one of three foods differing in bulk content (Control (C), wheat bran-based (WB) or sugar-beet-pulp-based (SBP)) in Period 1 on the subsequent daily rate of absolute food intake (FI), scaled food intake (SFI), live-weight gain (LWG), scaled live-weight gain (SLWG), food conversion efficiency (FCE), median visit duration, number of visits made in a day, total visit duration and feeding rate (FR) in Period 2 where pigs were given one of three foods differing in bulk content. The low bulk food is C, the wheatbran-based food is WB and the sugar beet pulp-based food is SBP.

Treatment											
Period	Period	FI	SFI	LWG	SLWG	FCE	Median	Visits	Total visit	Intake/	FR
1	2	(g day <sup>-1</sup> )	(g kg <sup>-1</sup> day <sup>-1</sup> )	(g day <sup>-1</sup> )	(g kg <sup>-1</sup> day <sup>-1</sup> )	(gain:intake)	visit	/day	duration	Visit	(g min <sup>-1</sup> )
							duration		(min day <sup>-1</sup> )	(g)	
							(secs)				
WB	C	2135	48.2	1014	22.3	0.478	22.0	94.0	58.3	25.0	38.0
SBP	C	1872	54.1	973	26.9	0.520	50.0	79.0	72.5	34.0	26.0
	WB	1717	40.1	847	20.6	0.498	24.0	156	90.0	11.0	20.0
SBP	WB	2390	66.8	960	26.1	0.403	29.0	181	99.2	14.0	25.0
	SBP	1169	27.6	588	14.3	0.527	25.0	114	82.8	10.0	15.0
WB	SBP	1646	38.7	787	18.6	0.481	60.0	90.0	144.7	19.0	12.0
s.e.d.		259.9	6.20	91.1	2.10	0.059	15.5	34.5	15.6	8.30	4.90
Significance		**	***	**	***	ns	ns	*	**	ns	**

#### 4.4.4 EFFECT OF RESTRICTING TIME OF ACCESS TO THE FEEDER ON PERFORMANCE AND STFB

Intake was reduced to a similar level on all three foods on the first day of restriction (Figure 4.1). A period of 10 days was sufficiently long for pigs fed C and WB to adapt to the new feeding regime. After only 5 days intake on C and WB had reached that before the restriction. However, on SBP intake did not return to the initial level within the 10-day period.

There was no effect of 6 h access on either intake or performance on C (Table 4.6), nor on median visit duration, total daily visit duration or feeding rate (Table 4.7). There was a reduction in SFI ( $P < 0.01$ ) and the number of visits made to the feeder in a day ( $P < 0.01$ ). The intake per visit was 1.84 times that on 24 h access ( $P < 0.05$ ).

On both WB and SBP absolute food intake ( $P < 0.001$ ), SFI ( $P < 0.05$  for WB and  $P < 0.001$  for SBP), performance ( $P < 0.001$  for LWG and  $P < 0.001$  for SLWG) and FCE ( $P < 0.05$  for WB and  $P < 0.001$  for SBP) were significantly reduced on 6 h access (Table 4.6). On SBP there was an increase in median visit duration ( $P < 0.01$ ) on 6 h access but this did not occur on WB. For WB and SBP the number of visits was reduced ( $P < 0.001$ ) on 6 h access. On WB total daily visit duration on 6 h access was 0.84 ( $P < 0.05$ ), and on SBP 0.80 ( $P < 0.001$ ), of that on 24 h access. There was no effect of reducing time of access to the feeder on intake per visit or feeding rate of pigs fed WB or SBP.

Feeding duration between 10:00 and 16:00 h was greater with 6 than with 24 h access ( $P < 0.05$  for C,  $P < 0.001$  for WB and SBP). Only on C was the daily feeding time on 6 h access not significantly reduced.

**Table 4.6.** The daily rate of absolute food intake (FI), scaled food intake (SFI), live-weight gain (LWG) and scaled live-weight gain (SLWG) of pigs fed one of three foods differing in bulk content in Period 3 compared to the average of Period 2 and 4. The low bulk food is C, the wheat bran-based food is WB and the sugar beet pulp-based food is SBP.

Food	Period	FI (g day <sup>-1</sup> )	SFI (g kg <sup>-1</sup> day <sup>-1</sup> )	LWG (g day <sup>-1</sup> )	SLWG (g kg <sup>-1</sup> day <sup>-1</sup> )	FCE (gain:intake)
C	Average 2 + 4	2131	42.6	905	15.9	0.420
	3	1956	36.0	800	14.7	0.414
	s.e.d.	141.9	1.84	141.8	2.60	0.057
WB	Average 2 + 4	2844	50.2	996	18.8	0.332
	3	2368	47.1	581	11.6	0.250
	s.e.d.	81.9	1.06	81.9	1.50	0.033
SBP	Average 2 + 4	2256	44.6	1054	19.4	0.471
	3	1712	32.7	454	8.80	0.271
	s.e.d.	81.9	1.06	81.9	1.50	0.033
s.e.d.for between food comparisons		235.5	2.15	118.2	2.00	0.054
Significance of effects						
Food		*	***	ns	ns	*
Period		***	***	***	***	***
Food*Period		ns	***	*	*	*

**Table 4.7.** The median visit duration, number of visits a day, total visit duration between 1000 and 1600hrs, intake per visit and feeding rate (FR) of pigs fed one of three foods differing in bulk content in Period 3 compared to the average in Period 2 and 4. The low bulk food is C, the wheat bran-based food is WB and the sugar beet pulp-based food is SBP.

Food	Period	Median visit duration (secs)	Visits/day	Total visit duration (min day <sup>-1</sup> )	Total visit duration 1000 - 1600 hrs (min)	Intake/Visit (g)	FR (g min <sup>-1</sup> )
C	Average 2 + 4	30.0	102	54.0	26.0	25.0	42.0
	3	40.0	72.0	40.9	40.9	46.0	48.0
	s.e.d.	10.8	9.50	9.80	5.70	9.70	3.00
WB	Average 2 + 4	26.0	189	86.6	43.2	16.0	35.0
	3	23.0	151	72.5	72.5	18.0	33.0
	s.e.d.	6.20	5.50	5.70	3.30	5.60	1.70
SBP	Average 2 + 4	56.0	109	146.3	79.3	23.0	16.0
	3	79.0	67.0	116.4	116.4	29.0	15.0
	s.e.d.	6.20	5.50	5.70	3.30	5.60	1.70
s.e.d. for between food comparisons		15.6	27.3	13.2	8.90	10.6	4.50
Significance of effects							
Food		*	**	***	***	ns	***
Period		*	***	***	***	ns	ns
Food*Period		ns	ns	ns	*	ns	ns

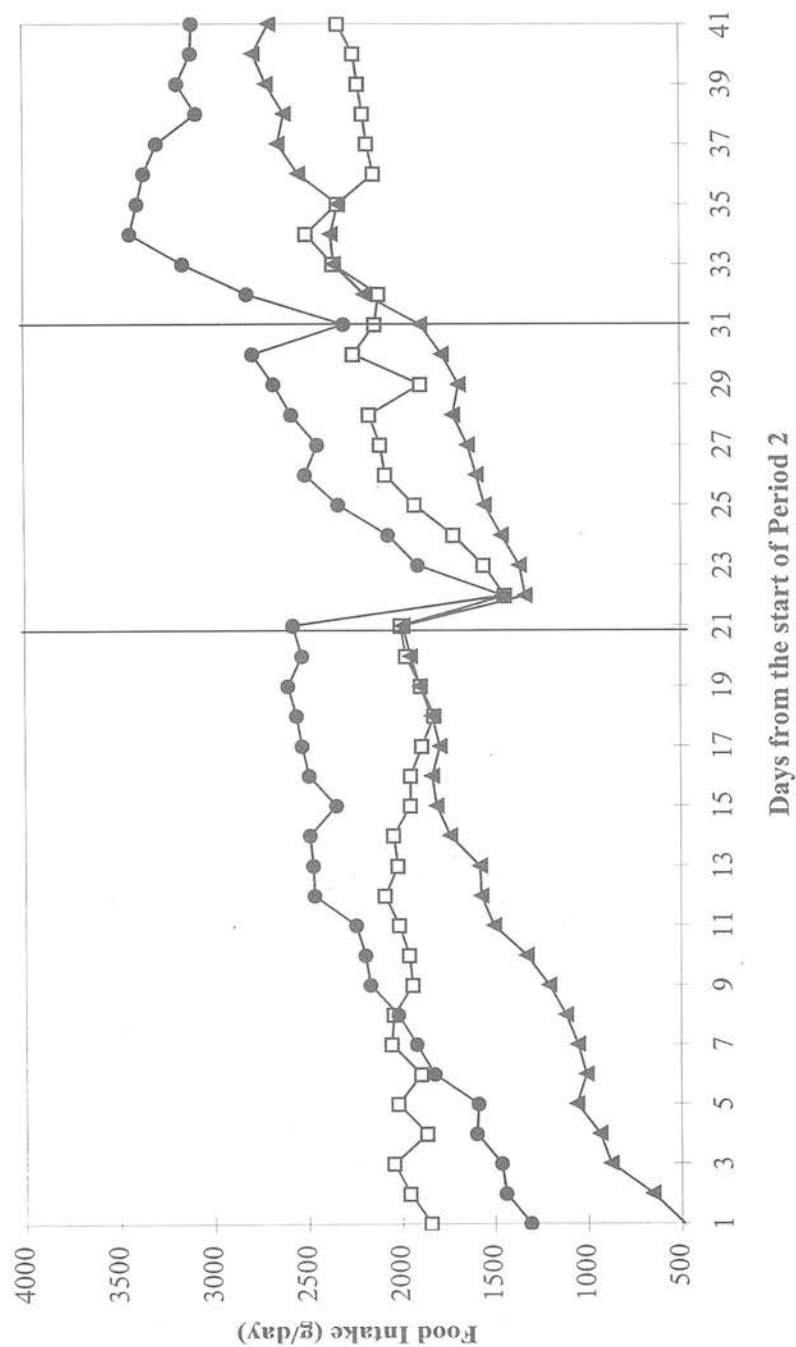
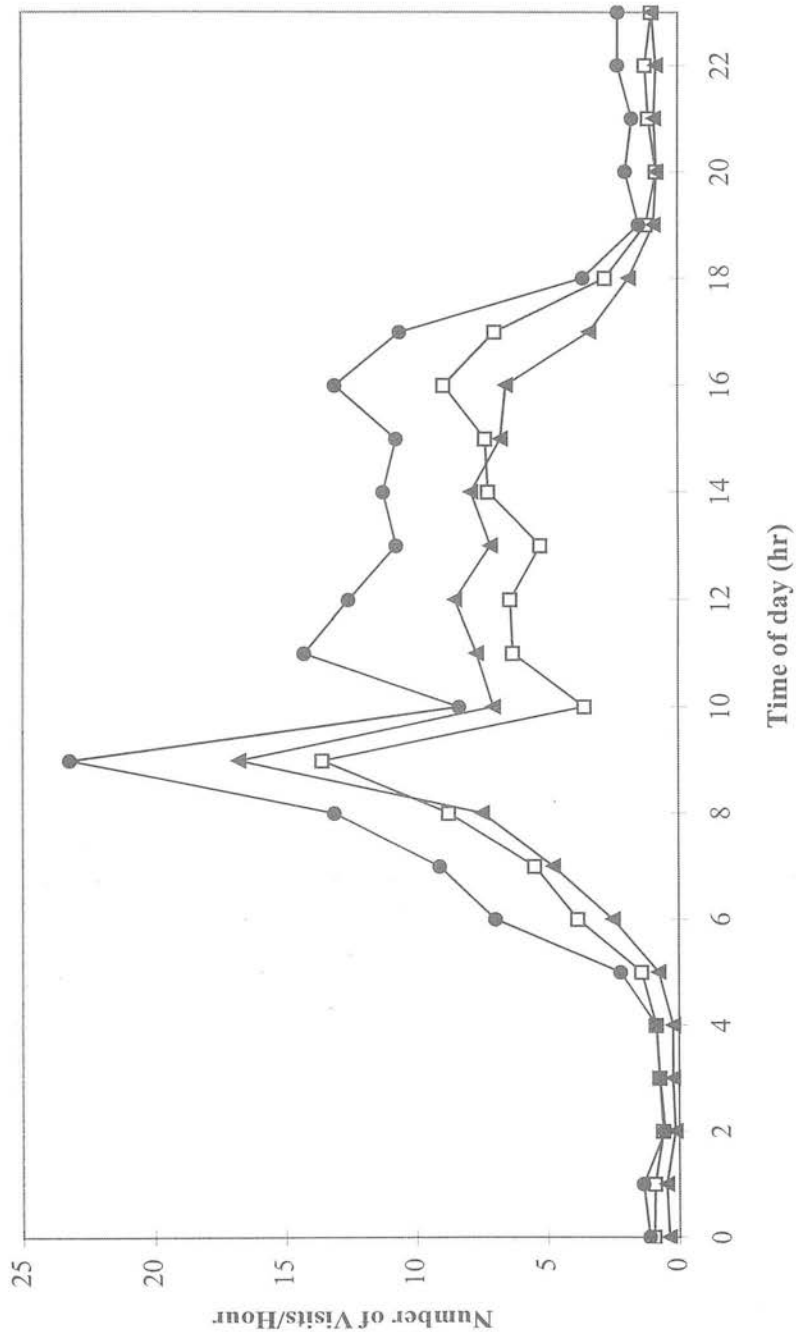


Figure 4.1. Changes in absolute food intake during Periods 2 (24 hours access to the feeder), 3 (6 hours access to the feeder) and 4 (24 hours access to the feeder) of the Control food (C) □, the wheat bran-based food (WB) ●, and the sugar-beet-pulp-based food (SBP) ▲. The vertical lines denote the end of a period.

#### 4.4.5 DISTRIBUTION OF VISITS IN A DAY

The way in which visits were distributed through the day on 24h access is shown in Figure 4.2. There was a peak of feeding activity at around 08:30 h, which coincided with the pigs being offered fresh food. A lower, but more prolonged, period of feeding activity was observed in the afternoon, before it dropped to a low level during the night.

On all foods there was a clear diurnal pattern of feeding with feeding activity lower during the night. Figure 4.2 shows that pigs fed WB and SBP did not extend feeding into the night. In Period 1 the proportions of visits that occurred during the night were C, 0.24, WB, 0.16 and SBP, 0.08 (s.e.d. 0.036). The proportions on WB and SBP were lower than on C ( $P < 0.05$  and  $P < 0.001$  respectively). In Periods 2 and 4 there was no effect of food on the proportion of visits that occurred during the night; C, 0.19; WB, 0.14 and SBP, 0.10 (s.e.d. 0.033) for Period 2 and C, 0.19; WB, 0.11 and SBP, 0.12 (s.e.d. 0.10) for Period 4.

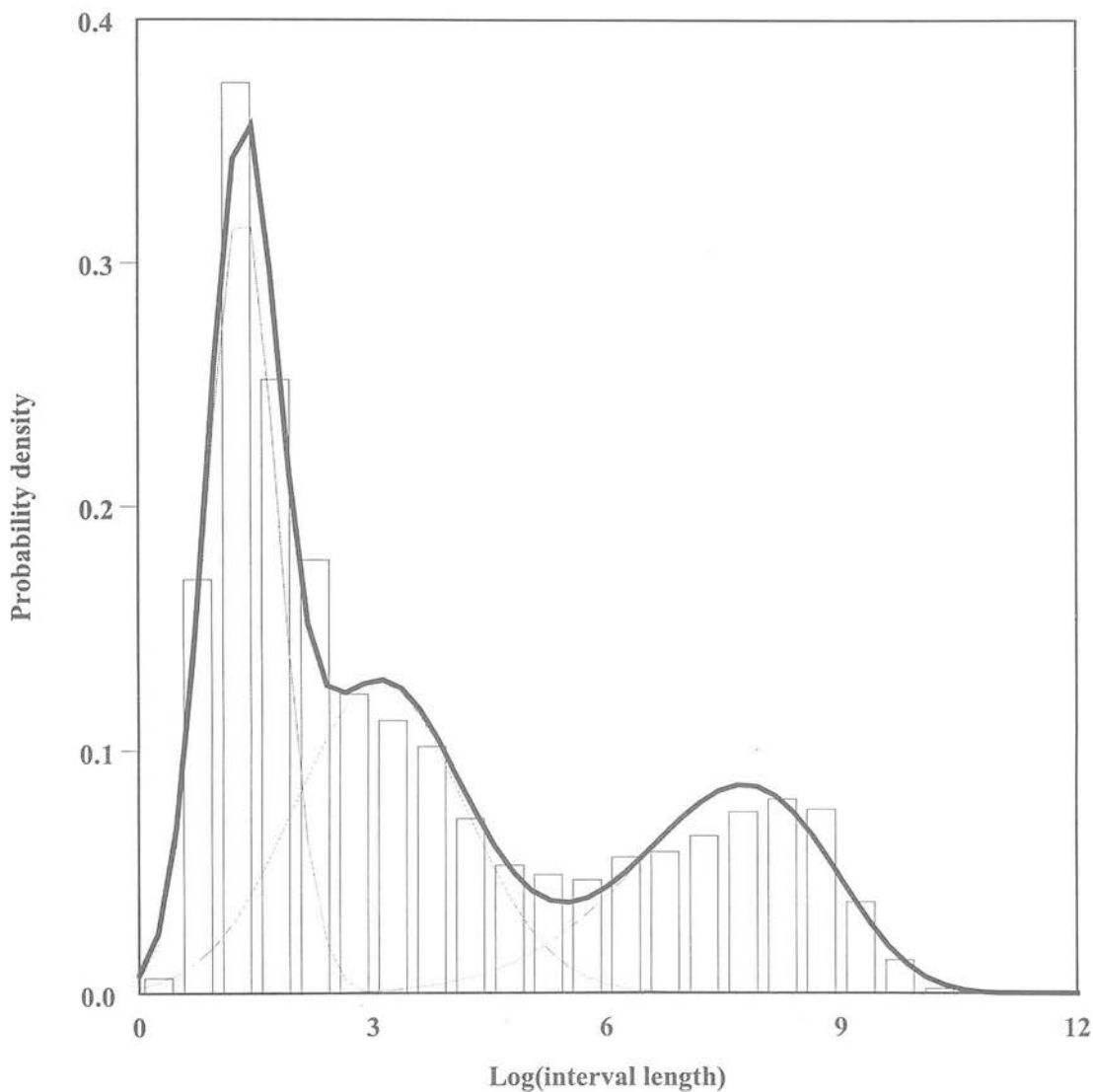


**Figure 4.2.** Distribution of visits throughout the day averaged across Periods 1, 2 and 4 (24 hours access to the feeder) on the Control (C) □, the wheat bran (WB) ●, and the sugar beet pulp food (SBP) ▲.

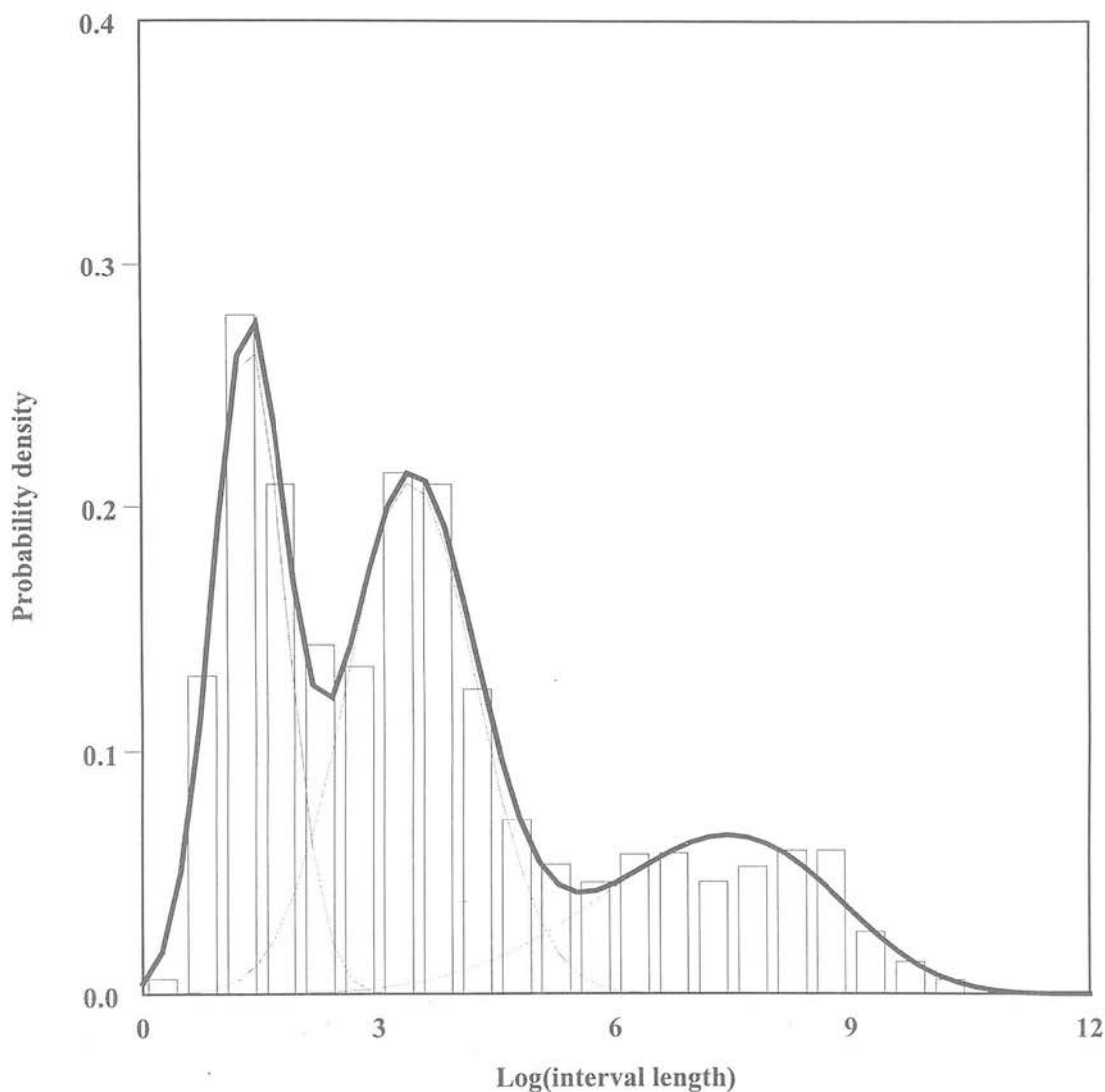


#### 4.4.6 DISTRIBUTIONS OF LOG TRANSFORMED INTERVAL LENGTHS

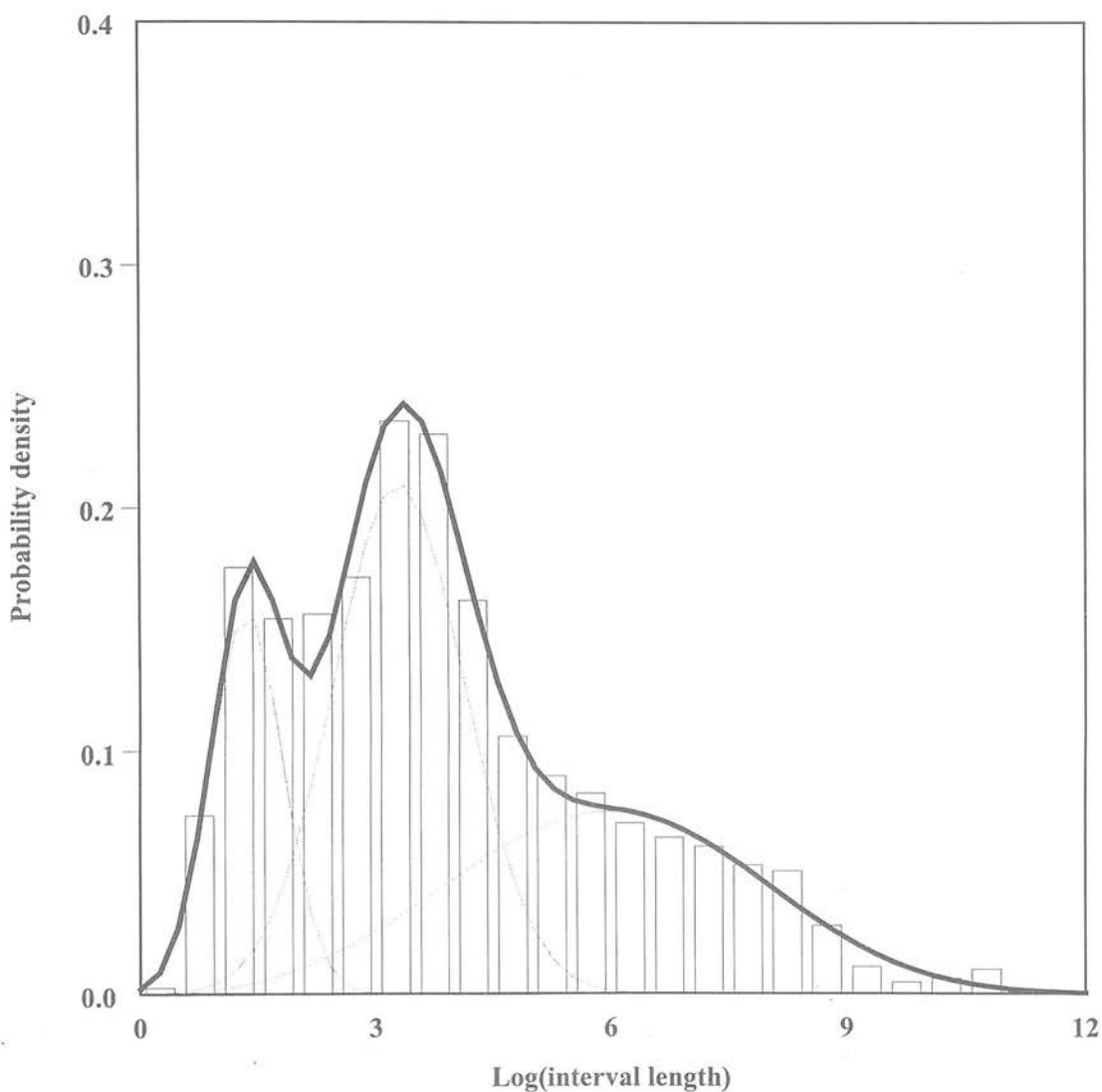
The distributions of the log-transformed intervals are in Figure 4.3 for Period 1, which had data representative of the whole experiment. The intermediate distribution represented 0.489 of the short intervals on C compared to 0.584 on WB and 0.710 on SBP (s.e.d. 0.0968, ns). If this distribution represents within meal drinking then pigs fed WB, and particularly those fed SBP, drink more during feeding than pigs fed C.



*Figure 4.3a. The distribution of the log-transformed lengths of intervals between visits to the feeder for pigs fed the control food (C) in Period 1. The first distribution is assumed to represent intervals within meals, the intermediate distribution is assumed to represent intervals within meals during which the drinker is visited and the last distribution is assumed to represent intervals occurring between meals. The thin black lines represent each individual distribution and the thick line represents the sum of the three populations.*



**Figure 4.3b.** The distribution of the log-transformed lengths of intervals between visits to the feeder for pigs fed the wheatbran food (WB) in Period 1. The first distribution is assumed to represent intervals within meals, the intermediate distribution is assumed to represent intervals within meals during which the drinker is visited and the last distribution is assumed to represent intervals occurring between meals. The thin black lines represent each individual distribution and the thick line represents the sum of the three populations.



**Figure 4.3c.** The distribution of the log-transformed lengths of intervals between visits to the feeder for pigs fed the sugar beet pulp food (SBP) in Period 1. The first distribution is assumed to represent intervals within meals, the intermediate distribution is assumed to represent intervals within meals during which the drinker is visited and the last distribution is assumed to represent intervals occurring between meals. The thin black lines represent each individual distribution and the thick line represents the sum of the three populations.

## **4.5 DISCUSSION**

### **4.5.1 EFFECT OF FOOD ON FOOD INTAKE AND PERFORMANCE**

The foods differed in bulk and it was expected that intakes and STFB would differ as a consequence. SBP was intended to limit both intake and performance. WB was expected to be less limiting. Intake and gain were reduced in pigs fed SBP for the main part of the experiment. In Period 1 intake on WB was similar to C. As WB was of poorer quality, gain was less. After the change over from Period 1 to 2 the pigs were maintained on the same food for the remainder of the experiment. It was expected that the longer the pigs spent on SBP and WB, and as they increased in size, the extent to which the food was limiting would be reduced (Chapter 2; Chapter 3); this was found to be the case. Intake on WB came to be higher than that on C with similar gains (Tables 4.3, 4.4 and 4.6). On SBP intake eventually increased so that gain was as high as on C (Table 4.6). Both these findings are consistent with previous work (Chapter 2; Chapter 3).

### **4.5.2 THE EFFECT OF FOOD ON STFB**

STFB was affected by food composition. On C it was similar to that observed in other work where pigs were fed a high quality food (Bigelow and Houpt, 1988; de Haer and de Vries, 1993). The effects of food bulk in the present work agree with previous work in gilts (Rushen *et al.*, 1999), dry sows (Brouns *et al.*, 1997), outdoor sows (Martin and Edwards, 1994) and Japanese quail (Savory, 1980), which has shown that foods high in bulk give lower feeding rates and more time spent eating. Feeding rate was reduced, and feeding time increased, more on SBP than on WB in agreement with (Ramonet *et al.*, 2000).

Mastication time is greater, and rates of consumption lower, in pigs on high bulk foods (Ramonet *et al.*, 1999, Brouns *et al.*, 1997). The increase in chewing time may

reflect differences in water holding capacity (WHC) between the foods (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). It has been suggested that increased chewing (and hence a greater saliva output) may be necessary to facilitate the swallowing of foods high in WHC, such as SBP (Brouns *et al.*, 1997). Pigs on WB and SBP would need a longer mastication time, and hence have a reduced feeding rate, compared to pigs on C, with the effects being greater on SBP than WB.

There were differences in STFB between WB and SBP. On WB there were significantly more visits of a significantly shorter duration. FR on SBP was lower than that on WB but visit duration was not increased sufficiently to equalise intake.

On WB the STFB changed after Period 1. In Period 1 a longer total daily feeding time was achieved by increasing median visit duration. Subsequently, a longer total daily feeding time was achieved through an increase in the number of visits made to the feeder. It is likely that the differences are related to individual differences in FR and that WB was not a limiting food after Period 1.

#### **4.5.3 DIURNAL PATTERNS OF FEEDING**

On all three foods (Figure 4.2) most feeding occurred during the day with little at night. The large peak in feeding during the morning coincided with the time that the pigs were offered fresh food as seen in previous work with pigs on low bulk foods (de Haer and Merks, 1992; Bornett *et al.*, 2000). The clear diurnal pattern on WB and SBP was not in agreement with H1 that there would be less diurnal variation on high bulk foods. If there is a bulk constraint to food intake, as is frequently assumed (Mraz *et al.*, 1957; Tsaras *et al.*, 1998; Kyriazakis and Emmans, 1999), then pigs on such foods would be expected to feed more regularly throughout the day and to extend their feeding into the night. We found neither. Physiological recognition of day and night is clearly a key element governing feeding behaviour.

It has been found that the diurnal pattern of feeding, and the inherent unwillingness of pigs to feed at night (or during the day in the case of rats), is overcome (at least on foods of low bulk content similar to C) in response to an increase in feeder pressure. When pigs were housed with 20 or 30 in a group the biphasic pattern of eating normally seen disappeared and feeding occurred throughout the night (Walker, 1991; Nielsen *et al.*, 1995). It is not clear why feeding was not extended into the night on the bulky foods used here. It could be that on such foods pigs are prevented from consuming food during the night due to the physical fill achieved during the day. The visits per hour on SBP gradually declined during the later half of the day (Figure 4.2), in contrast to pigs fed C and WB where feeding activity continued at a high level throughout the day. This pattern of feeding is consistent with the idea that during the course of the day pigs fed SBP were gradually approaching an upper limit to the capacity of their gastrointestinal for bulk. This explanation would imply a synchronicity between the pigs' diurnal rhythm and the gradual 'filling' of their gastrointestinal tract. This may be more than coincidence. Although not agreeing with our H1 our results agree with work in rats and pigs where the diurnal pattern of feeding was not altered on foods of high bulk (Johnson *et al.*, 1986; Walker, 1991; Nielsen *et al.*, 1995). There may be a common physiological mechanism that influences the effects of photoperiod and fibre on intake in rats and pigs even though one feeds during the day and the other at night.

#### **4.5.4 EFFECT OF RESTRICTING TIME OF ACCESS TO THE FEEDER ON STFB**

When access was reduced from 24 to 6 h a day it was hypothesised that on the bulky foods intake and performance would be reduced with the effect being greater on SBP than on WB. The results agreed with this hypothesis. On C STFB changed so that intake and performance were maintained on 6 h access mainly by increasing food intake per visit in agreement with previous work (Bornett *et al.*, 2000). Pigs fed SBP and WB, however, did not maintain intake and performance reflecting an inability to alter STFB with no increase in food intake per visit.

Pigs fed high bulk foods are thought to remain fuller for longer (Day *et al.*, 1996; Brouns *et al.*, 1997; Meunier-Salaun *et al.*, 2001) and, therefore physical fill may prevent the total daily feeding time achieved in twenty four hours being achieved in six hours.

#### **4.5.5 EFFECTS OF A CHANGE OF FOOD ON STFB**

The response of feeding behaviour to a change in food was rapid and occurred in the way that would have been expected to occur if intake was constrained. The changes were in agreement with previous work (Savory, 1980; Brouns *et al.*, 1997; Rushen *et al.*, 1999, Ramonet *et al.*, 2000), where, as seen here, the feeding of a high bulk food increased total daily feeding time and reduced feeding rate.

The ability of pigs to consume more of a bulky food following a similar food agrees with other work (Kyriazakis and Emmans, 1995). It is likely to be related to an increase in the length and size of the gastrointestinal tract (Hansen *et al.*, 1992; Kyriazakis and Emmans, 1995; Pluske *et al.*, 1998). The gastrointestinal tracts of pigs with prior experience of bulky foods would be expected to be better adapted to such foods and thus be able to eat more of another high bulk food fed subsequently. The results of the experiment were in agreement with this hypothesis.

#### **4.5.6 DISTRIBUTION OF THE LOG - TRANSFORMED INTERVAL LENGTHS**

The model of Yeates (2001) was fitted to the log transformed interval data to allow estimation of differences in the size of the intermediate population. This was determined as the number of intervals within the intermediate population as a proportion of the total number of short (or within meal) intervals. In previous work (Tolkamp and Kyriazakis, 1999) the intermediate population was assumed to be



associated with drinking behaviour. The mean interval length of the intermediate distribution was commensurate with visits by cows to the drinker within a meal supported by concurrent behavioural observations (Tolkamp and Kyriazakis, 1999). Drinking behaviour in pigs is also known to be closely related to meals with about one third of drinking occurring during meals on high quality foods (Bigelow and Houpt, 1988). In pigs the mean interval length of the intermediate distribution was shown to be consistent with drinking intervals within a meal (Morgan *et al.*, 2000a) and it seems reasonable to assume that the intermediate distribution is associated with drinking.

It was clear that there were significant differences between the foods in the size of the intermediate distribution reflecting differences in bulk content as measured by water holding capacity (WHC). Bulky foods could increase the demand for water within a meal so that pigs on SBP (Tsaras *et al.*, 1998; Chapter 2) would show more within meal drinking.

## **4.6 CONCLUSIONS**

The foods used differed in bulk content and affected food intake and short term feeding behaviour (STFB). The differences were consistent in part with those expected to occur if a bulk constraint to food intake existed. Contrary to expectation, a higher bulk content had no significant effect on the diurnal intake pattern of pigs given twenty four hours access to food; the reason for this, and its physiological basis, remains unclear. Pigs fed the higher bulk foods did not maintain food intake and performance when time of access to the feeder was reduced mainly due to the absence of any adaptive change in STFB. It is argued that this was the result of physical limitations although this cannot strictly be concluded. When pigs were changed from a food with a higher, to one of a lower bulk content, or vice versa, there was a rapid change in STFB to become appropriate to the new food. Previous experience of a bulky food facilitated the intake of another bulky food in a subsequent period, a result consistent with the concept that intake is physically constrained. Analysis of the frequency distribution of intervals between visits to the feeder suggested large differences in drinking behaviour between pigs fed foods differing in bulk. The observed differences in feeding pattern between treatments are consistent with the idea that food intake on bulky foods is physically constrained. It is concluded that a physical constraint may play an important role in the regulation of food intake on poor quality or high bulk foods.

# **CHAPTER 5**

**The relationship between liveweight  
and food intake on constraining,  
bulky foods in pigs**

## **5.1 ABSTRACT**

Between 12 and 40 kg the capacity for food bulk has been shown to be directly proportional to liveweight. In this experiment pigs between 12 and 120 kg were used to develop a relationship for the whole relevant weight range. High bulk foods, intended to limit growth, were fed for 21 days at 12, 36 and 108kg. A food with 60% sugar beet pulp (SBP<sub>60</sub>) was fed at 12 and 36kg and one with 80% sugar beet pulp (SBP<sub>80</sub>) at 108kg. Control pigs were fed on a low bulk food C at all weights. After 21 days the pigs were slaughtered and measurements made on the gastrointestinal tract (GIT). The effect of previous nutritional history on the intake of high bulk foods was also investigated in two treatment groups where SBP<sub>60</sub> was fed from a weight of either 36kg or 72kg prior to SBP<sub>80</sub> being fed at 108kg. After allowing for the effects of a change of gut fill, daily liveweight gain was less at all weights on the high bulk foods than on C. At all weights the high bulk foods caused a significant increase in the weights of the stomach, large intestine, caecum and gut fill. Effects on the weight of the small intestine were small. Previous nutrition had no significant effect on the adapted performance, or on the size of the GIT, of pigs fed SBP<sub>80</sub> at 108kg, but pigs previously fed SBP<sub>60</sub> were able, initially, to consume significantly more of SBP<sub>80</sub> than pigs with no previous experience of a bulky food. The rule that constrained food intake is proportional to liveweight did not hold for pigs that were greater than 40kg, as the bulk intake per kg liveweight was not constant but decreased with an increase in liveweight beyond 40 kg. The relationship between liveweight (W, kg) and the absolute capacity for bulk (Cap, kg water holding capacity day<sup>-1</sup>) was well described by the quadratic function  $Cap = (0.230.W) - (0.000476.W^2)$ . The value of Cap reaches a maximum when W = 242 kg. The combined weights of the large intestine and caecum (WLIC) changed with W in ways that were similar to the way in which Cap changed. In addition the ratio of Cap divided by WLIC was more or less constant across the weight range of interest. This provides some evidence that the combined weight of the large intestine and the caecum are linked to capacity for food bulk.

## **5.2 INTRODUCTION**

A change to a food of higher bulk content initially causes a reduction in food intake in pigs (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). Intake then gradually increases with adaptation to reach an equilibrium intake that is appropriate to the food being fed. On a constraining food this equilibrium level of intake will be less than the desired level of food intake, which is that required for the genetic potential to be achieved (Kyriazakis and Emmans, 1999). The amount of a bulky food that an animal can eat depends on its capacity for bulk and the bulk content of the food. In young growing pigs the maximum capacity for food bulk at a time was found to be directly proportional to liveweight (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998; Chapter 2). For pigs between 12 and 40kg the value for the constant of proportionality was found to be 0.17 (Kyriazakis and Emmans, 1995) and 0.23 (Tsaras *et al.*, 1998) units of water holding capacity  $\text{kg liveweight}^{-1} \text{ day}^{-1}$ . A recent model (Chapter 6) proposed a higher value of 0.27. Water holding capacity (WHC) is a measure of a foods ability to hold water within its matrix and has been shown to be a good indicator of the bulk content of the food (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). The differences in the value of the constant of proportionality between experiments could be a reflection of the methodological differences in the measurement of WHC.

The way in which the capacity for bulky foods changes with weight above 40 kg is not clear. There is no *a priori* reason to assume that the scaling rule proposed by Kyriazakis and Emmans (1995) will hold in pigs greater than 40kg liveweight. The applicability of the work completed in young growing pigs for use in more mature pigs needs investigation if predictive equations that can be used across the whole relevant weight range are to be developed.

On high bulk foods the equilibrium level of intake reflects the animals maximum capacity for that food and it is the equilibrium intake that will be used in predictive equations (Chapter 6). The time taken to adapt fully to a new food also needs to be

known. In pigs between 12 and 40kg adaptation takes between 7 and 14 days (Owen and Ridgman, 1968; Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998; Chapter 2). The length of time required for adaptation to a constraining food in pigs greater than 40kg is not known and may also be affected by previous nutritional history. Previous experience of a bulky food reduces the time taken to adapt to, and increases the intake of, bulky foods (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998).

An experiment was designed to determine how the capacity for bulk changed with weight in pigs by feeding high bulk foods formulated to be constraining at the weights of 12, 36 and 108 kg at which they were fed. The effects of previous nutritional history on the intake of high bulk foods were also investigated.

## **5.3 MATERIALS AND METHODS**

### **5.3.1 ANIMALS AND HOUSING**

Thirty-two (19 females and 13 entire males from 5 litters) commercial hybrid pigs (Large White x Landrace, Cotswold, U.K.) were placed immediately after weaning at 4 weeks of age at 9.3 (s.d. 1.24) kg into individual pens in the experimental unit. The experimental unit consisted of four identical rooms, each with its own lighting, heating and ventilation system. Initially each room contained eight pens, which were arranged in four sets of two. Each pen measured 2 x 1m and had a metal bowl drinker and a feeding trough. The pens had concrete floors and were provided with straw. As the number of pigs on the experiment was reduced (see experimental design) and the pigs increased in size, the middle partition, one drinker and one feeding trough were removed from each set of two pens. The number of pens in each room was thus reduced to four with each pen now measuring 2 x 2m. The target temperature, throughout the experiment, was 18°C. The actual average temperatures achieved in each of the four rooms were, 18.0 (s.d. 1.4) °C, 18.1 (s.d. 1.4) °C, 18.2 (s.d. 1.4) °C, and 18.0 (s.d. 1.3) °C.

### **5.3.2 FOODS**

Three foods were formulated and made into pellets (Table 5.1). The control food (C) was low in bulk as measured by water-holding capacity (WHC). It was based on micronised wheat and contained 12.9 MJ digestible energy (DE) and 212g crude protein (CP) per kg of fresh food. The other two foods were formulated to have high bulk contents as measured by WHC and contained either 600g kg<sup>-1</sup> (SBP<sub>60</sub>) or 800g kg<sup>-1</sup> (SBP<sub>80</sub>) unmolassed sugar beet pulp. SBP<sub>60</sub> had 11.3 MJ DE and 163g CP, and SBP<sub>80</sub> 10.7 MJ DE and 156g CP per kg of fresh food. The foods were supplemented with synthetic amino acids, vitamins and minerals to give similar calculated ratios of protein, essential amino acids, vitamins and minerals to DE. It was expected that the

pigs given food C would be able to eat and perform according to their genetic potential. Foods SBP<sub>60</sub> and SBP<sub>80</sub> were intended to limit performance at the liveweights at which they were fed (Tsaras *et al.*, 1998; Chapter 2 and 3).

The foods were analysed for gross energy (GE), dry matter (DM), CP, diethyl ether extract, ash, crude fibre (CF), acid detergent fibre (ADF; Goering and van Soest, 1970) and neutral detergent fibre (NDF; Robertson and van Soest, 1977) and WHC. WHC was determined using the methodology of Tsaras *et al.* (1998) with one difference. The samples were centrifuged to a constant weight after soaking for 24hrs as, in previous work (Chapter 3), foods based on sugar beet pulp did not form a solid pellet at the bottom of the test tube after 15min centrifugation. The chemical composition and chemical analyses of the foods are given in Table 5.1.



**Table 5.1.** *The composition and chemical analyses (g/kg as fed) of the three experimental foods: control (C), and sugar beet pulp - based (SBP<sub>60</sub> and SBP<sub>80</sub>) foods.*

	Food		
	C	SBP <sub>60</sub>	SBP <sub>80</sub>
<b>Ingredients (kg/tonne)</b>			
Micronised Wheat	752.9	188.1	0.0
Sugar beet pulp	0.0	600.0	800.0
Fishmeal	180.0	160.2	153.6
Sogipro	20.0	5.0	0.0
Mineral/vitamin premix†	12.5	12.5	12.5
Maize oil	20.0	20.0	20.0
Lysine hydrochloride	4.1	1.6	0.75
DL-methionine	0.75	0.80	0.75
L-threonine	2.4	1.3	0.8
L-tryptophan	0.3	0.6	0.6
Monosodium phosphate	7.0	10.0	11.0
Total	1000.0	1000.0	1000.0
<b>Composition (g or MJ/kg fresh food)</b>			
Dry matter	873.9	872.2	869.5
Crude protein	212.4	163.1	155.6
Ether extract	39.1	25.6	35.8
Ash	53.7	70.2	83.6
Crude fibre	19.8	108.2	132.2
Acid detergent fibre	29.1	137.8	159.9
Neutral detergent fibre	118.9	299.2	340.8
Water-holding capacity (g water per g dry food)	3.04	6.26	8.14
Digestible energy (MJ/kg)*	12.9	11.3	10.7
Gross energy (MJ/kg)	16.4	15.7	15.3

† A protein supplement prepared from extracted soya beans with a CP of 700g/kg

\* Calculated

### **5.3.3 EXPERIMENTAL DESIGN**

The pigs were randomly allocated to one of eight treatment groups, a room within the experimental accommodation and to a pen within the room. Randomisation allowed for both sex and litter origin. The pigs were given 5 days to adapt to the

experimental accommodation before the start of the experiment. During this time they were fed a high quality commercial pig food, containing 215g protein per kg (Easiwean, BOCM Pauls Ltd, Ipswich) *ad libitum*. As each pig (apart from those on T1) reached 12kg they were put onto C. On T1 the pigs were fed SBP<sub>60</sub> from a liveweight of 12kg for a period of 21 days. On T2 the pigs were fed C until they attained an average liveweight which was the same as the end weight predicted to be achieved on T1. On T3 the pigs were fed SBP<sub>60</sub> from a liveweight of 36kg for a period of 21 days. On T4 the pigs were fed C until they attained an average liveweight which was the same as the end weight predicted to be achieved by the pigs on T3. On T5 the pigs were fed SBP<sub>80</sub> from a liveweight of 108kg for a period of 21 days. On T6 the pigs were fed C until they attained an average liveweight which was the same as the end weight predicted to be achieved by the pigs on T5. On T2, T4 and T6 variation in slaughter weight was introduced around the fixed mean by choosing weights of  $\pm 1$  and  $\pm 3$  kg (for T2 and T4) and  $\pm 3$  and  $\pm 6$  kg (for T6).

The period of 21 days used on SBP<sub>60</sub> and SBP<sub>80</sub> was considered to be long enough to allow the pigs to become fully adapted to these foods (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998), and to allow a further 7-day period during which equilibrium intake could be recorded. According to the results of previous work (Tsaras *et al.*, 1998; Whitemore *et al.*, 2001a) SBP<sub>60</sub> was expected to be limiting at 12 and 36kg. As the pigs of 108kg were expected to be able to cope better with bulky foods because of their larger GIT size a food with a higher SBP content was used at this weight (SBP<sub>80</sub>). T1, T3 and T5 were used to determine the effect of maturity on the capacity for bulk. The comparison of T1, T3 and T5 with the control treatment groups T2, T4 and T6 respectively determined if the high bulk foods were limiting for the weight at which they were fed.

On T7 the pigs were fed C to 36kg and then SBP<sub>60</sub> from 36kg to 108kg, at which weight they were changed to SBP<sub>80</sub> for a period of 21 days. On T8 the pigs were fed C to 72kg and then SBP<sub>60</sub> from 72kg to 108kg, at which weight they were changed to

SBP<sub>80</sub> for a period of 21 days. Treatments 6, 7 and 8 allowed any effects of previous nutritional history on intake, performance and the size of the GIT to be determined. After the period of 21 days on either SBP<sub>60</sub> (T1 and T3) or SBP<sub>80</sub> (T5, T7, and T8), or when the appropriate liveweight was reached (T2, T4, and T6), the pigs were slaughtered and measurements made on the GIT.

#### **5.3.4 MANAGEMENT AND MEASUREMENTS**

The pigs were fed *ad libitum* with refusals at 0.10 - 0.15 of intake. Refusals were removed from the troughs each morning, weighed and their DM determined by oven drying at 80°C for 24 hrs. The DM was then used to determine the fresh weight of the food consumed. Fresh food was added to the troughs each day after the refusals had been removed. The pigs were weighed at the same time twice a week. Temperature was recorded twice a day by means of a minimum/maximum thermometer. The pens were cleaned out and fresh straw added three times a week.

On the day of slaughter the pigs were weighed and food refusals removed at 08.00 h. No fresh food was given. The pigs were killed at 13.00 h by exsanguination after electrical stunning. Immediately after slaughter the liver and entire GIT were removed. Ligatures were used to separate the GIT into four segments: stomach, small intestine, large intestine and caecum. After removing and weighing the mesentery, each section was weighed full. The contents of each section were then emptied and the empty sections re-weighed. Total gut fill was calculated as the difference between the full and empty weights of the tract. Muscle and fat depths were measured with a ruler at the twelfth rib.

### 5.3.5 STATISTICAL ANALYSIS

#### *5.3.5.1 EQUILIBRIUM INTAKE*

It was expected that by the last 7 days of the 21-day period equilibrium intake on the bulky foods would have been reached (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). To test whether or not equilibrium intake had been reached scaled food intake (SFI g kg<sup>-1</sup> liveweight day<sup>-1</sup>) was regressed on time using both a linear (SFI =  $a_1 + b_1.t$ ) and a quadratic (SFI =  $a_2 + b_2.t + c_2.t^2$ ) function. To determine which regression provided the best fit to the data the residual error mean squares (rms) from the two regression equations were compared.

#### *5.3.5.2 ANALYSIS OF DATA*

The data from each of the three weights were analysed as a completely randomised design in Minitab (Minitab Incorporated, 1998), using a general linear model (GLM) to test for the effects of treatment. The variables were: food intake, SFI, liveweight gain, liveweight gain per kg d (SLWG), and the weights of the empty stomach, the small and large intestines, the caecum, the gut fill, and the mesentery. The muscle and fat depths were also analysed. The fixed factor in the model was treatment. For T1, T3, T5, T7 and T8 (n = 4) the average food intake and LWG for the last 7 days of the 21-day period were used for the analysis. These data were compared with the average food intake and LWG of the pigs fed C during the last 7 days before the average slaughter weight of the pigs on the relevant SBP treatment group was achieved. In this way the data from pigs fed SBP<sub>60</sub> at 12kg (T1) were compared with the data from 28 control pigs (the data of 2 pigs with abnormally low growth rates at this time were removed from this group prior to analysis, leaving 26). The data from pigs fed SBP<sub>60</sub> at 36kg (T3 and T7) were compared with the data from 16 pigs on C and the data from pigs fed SBP<sub>80</sub> at 108kg (T5, T7 and T8) were compared with the data from 4 pigs on C. As the pigs on T7 and T8 were also fed SBP<sub>60</sub> at an

intermediate weight of 72kg the data from these pigs were also compared with data from pigs fed C at a comparable weight.

The data on the GIT were also scaled to liveweight (Kyriazakis and Emmans, 1995) to allow comparisons across degrees of maturity to be made. For comparisons of the GIT and differences in the rate of change in gut fill (see Discussion) the number of animals in each treatment group was 4. The rate of change in gut fill was calculated as the rate of change in food intake during the last 7 days multiplied by the gut fill equivalent of the food fed. An adjusted LWG (aLWG) was then estimated as LWG minus the rate of change in gut fill. The gut fill at 72kg was estimated using the data from the pigs at 12, 36 and 108kg as gut fill equivalent on C and SBP<sub>60</sub> did not differ between weights. Calculating gut fill in this way meant that no statistical analysis of the data for aLWG at 72kg was possible.

To determine the relationship between capacity for bulk and liveweight across degrees of maturity, food intake (both absolute and scaled) was compared on a WHC basis i.e. the average intake of a food at each degree of maturity was multiplied by the WHC of the food being fed. This took account of the fact that foods of different bulk content were fed at different degrees of maturity. The capacity for bulk was calculated as  $FI \text{ (kg d}^{-1}\text{)} \times WHC \text{ (g g food}^{-1}\text{)}$ . This was also divided by the liveweight, kg, to derive the scaled capacity per kg. Differences in capacity for bulk between degrees of maturity were compared in Minitab using a GLM; the fixed factor in the model was liveweight.

## **5.4 RESULTS**

### **5.4.1 AVERAGE SLAUGHTER WEIGHTS**

The similarity in average slaughter weights for paired treatments was achieved (Table 5.2).

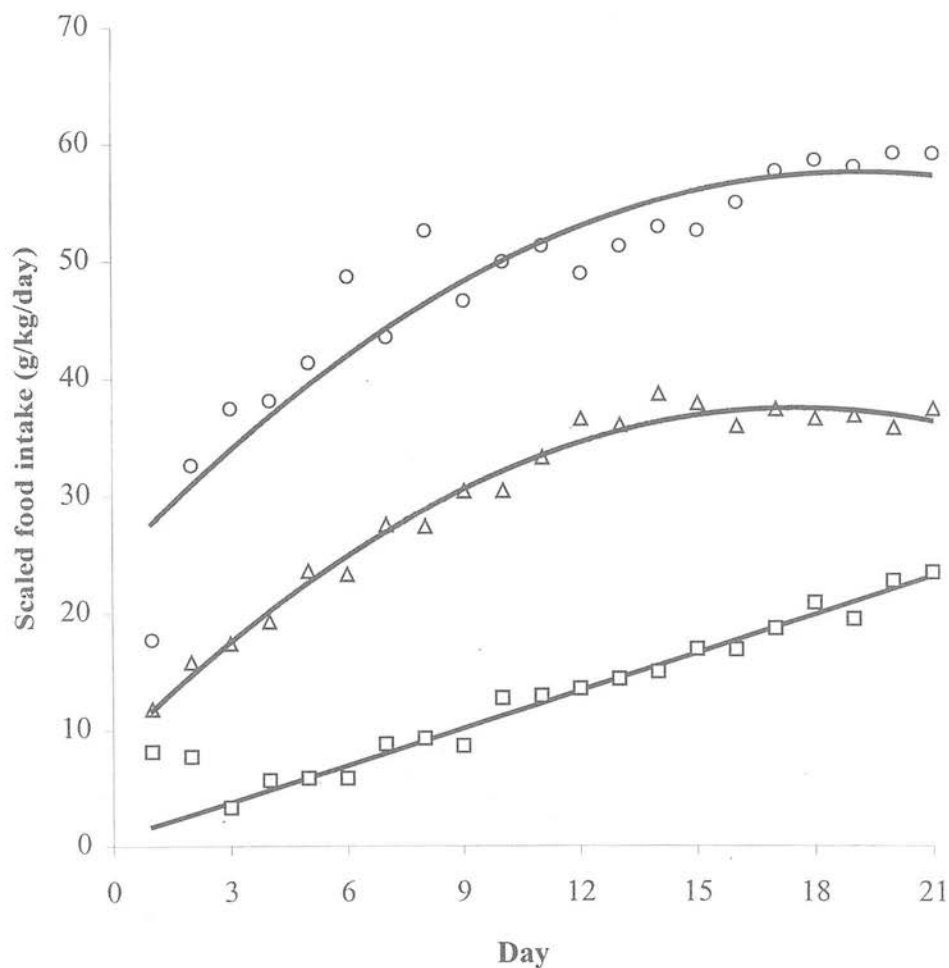
**Table 5.2** *The slaughter weight of pigs given access to one of three foods differing in sugar beet pulp content (control, 60% sugar beet pulp (SBP<sub>60</sub>) and 80% sugar beet pulp (SBP<sub>80</sub>)) at one of three different degrees of maturity (12, 36 and 108kg), N = 4 for each group.*

Treatment	Final Weight (kg)	s.d.
1 - SBP <sub>60</sub> 12kg	21.7	1.79
2 - Control	21.8	1.30
3 - SBP <sub>60</sub> 36kg	47.3	1.65
4 - Control	47.1	1.59
5 - SBP <sub>80</sub> 108kg	119.6	4.39
6 - Control	119.1	1.44
7 - SBP <sub>60</sub> 36kg, SBP <sub>80</sub> 108kg	121.0	4.64
8 - SBP <sub>60</sub> 72kg, SBP <sub>80</sub> 108kg	120.6	2.46

### **5.4.2 EQUILIBRIUM INTAKE**

Figure 5.1 shows the scaled food intake of pigs fed SBP<sub>60</sub> at 12kg (T1), SBP<sub>60</sub> at 36kg (T3) and SBP<sub>80</sub> at 108kg (T5) over time. At 12 and 36kg the rate of increase decreased over time so that, by the end of the period, scaled food intake had become

close to constant. However, at 108kg the pigs on SBP<sub>80</sub> continued to increase their scaled intake throughout the whole of the period and there is no indication that an equilibrium intake had been reached after 21 days. For both SBP<sub>60</sub> fed at 12kg and SBP<sub>60</sub> fed at 36kg a quadratic regression fitted the data significantly better than a linear one ( $P < 0.01$ ). A quadratic regression (rms 0.79) for SBP<sub>80</sub> fed at 108kg was no better than a linear one (rms 0.74).



**Figure 5.1.** Scaled food intake ( $\text{g kg}^{-1} \text{ day}^{-1}$ ) of pigs fed a 60% sugar beet pulp food at 12kg ( $\circ$ ), a 60% sugar beet pulp food at 36kg ( $\Delta$ ) or an 80% sugar beet pulp food at 108kg ( $\square$ ), for a period of 21 days. The black line is that fitted by the quadratic function  $y = 24.327 + 3.4889x - 0.091x^2$  for 12kg,  $y = 8.4299 + 3.3238x - 0.0949x^2$  for 36kg and  $y = 0.6450 + 1.0437x + 0.001628x^2$  for 108kg.

### 5.4.3 THE EFFECT OF FOOD ON PERFORMANCE AND GASTROINTESTINAL CHARACTERISTICS

The performance of pigs fed a high bulk food at 12, 36, 72 or 108kg during the last 7 days of the 21-day period is given in Table 5.3. Pigs fed SBP<sub>60</sub> at 12kg (T1) consumed significantly more food, but grew significantly slower than pigs fed C at the same weight. Liveweight gain (LWG) on SBP<sub>60</sub> was 0.80 and scaled liveweight gain (SLWG) was 0.81 of that on the control food. These results suggest that, as intended SBP<sub>60</sub> was a constraining food at 12kg.

There was no significant difference in the food intake, LWG, scaled food intake (SFI), SLWG or FCE of pigs fed SBP<sub>60</sub> at 36kg (T3) compared to those fed C at the same weight. In the absence of any significant reduction in LWG it cannot be concluded that SBP<sub>60</sub> was a constraining food at 36kg, as it had been intended to be.

The data from T7 and T8 were used to provide an estimate of the food intake and performance of pigs fed SBP<sub>60</sub> at the intermediate weight of 72kg. The food intake and performance on SBP<sub>60</sub> at 72kg were not significantly different to those achieved on C. Therefore, SBP<sub>60</sub> cannot be said to be a limiting food at 72kg.

Previous nutritional history (T5, T7 and 8) had no significant, or appreciable, effects on the adapted intake and performance of pigs fed SBP<sub>80</sub> at 108kg. While the pigs on T5 did not achieve equilibrium within the 21-day period (Figure 5.1) those on T7 and T8 with previous experience of a bulky food did achieve equilibrium in the last 7 days of the 21-day period (Figure 5.2). The data (Table 5.3) from T5, T7 and T8 were thus combined to give a better estimate of the performance able to be achieved on SBP<sub>80</sub>. As the LWG on SBP<sub>80</sub> was not significantly less than that on C it cannot be concluded that SBP<sub>80</sub> was a constraining food at 108kg.

The effects of the different treatments on the empty weight of the gastrointestinal tract (GIT) are given in Table 5.4. Again, there was no effect of previous nutritional



history on any measure so the data from T5, T7 and T8 (all pigs fed SBP<sub>80</sub> at 108kg) were combined. At all three degrees of maturity the high bulk foods caused significant increases in the weights of the stomach, the large intestine and gut fill compared to C. The high bulk foods led to a significant increase in the weight of the caecum at 12 and 36kg only. The pigs fed SBP<sub>80</sub> at 108kg had a caecum weight that was 1.38 times that on C, but this difference was not statistically significant. At 12kg the high bulk food caused a small but significant increase ( $P < 0.05$ ) in small intestine weight. No such effect was seen at either 36 or 108kg. There was no effect of treatment on either muscle depth or the weight of the mesentery at 12, 36 or 108kg. Pigs fed the bulky foods had a reduced P2 fat depth at all weights although this was not significant at 12 kg.

**Table 5.3** The means for food intake, liveweight gain (LWG), scaled food intake (SFI), scaled liveweight gain (SLWG) and food conversion efficiency (FCE) of pigs given access to one of three foods differing in sugar beet pulp content (control, 60% sugar beet pulp (SBP<sub>60</sub>) and 80% sugar beet pulp (SBP<sub>80</sub>)) at 12, 36 or 108kg. The data are for the last 7 days before slaughter for pigs fed the SBP foods, for the pigs fed the control food they are for the last 7 days before the liveweight closest to the average slaughter weight of the pigs fed SBP.

Treatment	N	Food Intake (g day <sup>-1</sup> )	LWG (g day <sup>-1</sup> )	SFI (g kg <sup>-1</sup> day <sup>-1</sup> )	SLWG (g kg <sup>-1</sup> day <sup>-1</sup> )	FCE
Control	26	927	743	47.8	38.3	0.805
SBP <sub>60</sub> 12kg	4	1103	608	56.6	31.2	0.570
s.e.d.		65.8*	40.8**	3.76*	2.6*	0.0496***
Control	16	1809	892	41.4	20.4	0.496
SBP <sub>60</sub> 36kg	8	1695	760	37.9	17.0	0.462
s.e.d.		125.3	74.8	2.93	1.74	0.0459
Control	8	2477	1103	31.6	14.1	0.447
SBP <sub>60</sub> 72kg	8	2297	997	29.0	12.6	0.441
s.e.d.		227.6	96.0	2.93	1.27	0.0284
Control	4	3095	1012	26.8	8.75	0.325
SBP <sub>80</sub> 108kg	12	2692	947	23.1	8.1	0.355
s.e.d.		181.4*	135.4	1.55	1.15	0.0519

**Table 5.4.** The empty weights of the gastrointestinal tract sections, gut fill and carcass depth of muscle and fat of pigs given access to one of three foods differing in sugar beet pulp content (control, 60% sugar beet pulp (SBP<sub>60</sub>) and 80% sugar beet pulp (SBP<sub>80</sub>)) at 12, 36 or 108kg.

Treatment	N	Stomach weight (g)	Small intestine weight (g)	Large intestine weight (g)	Caecum weight (g)	Gut fill (g)	Mesentery (g)	Muscle (mm)	Fat (mm)
Control	4	120.0	730.0	235.0	20.0	800.0	130.0	32.5	3.50
SBP <sub>60</sub> 12kg	4	230.3	840.5	517.3	62.8	2518.7	128.3	31.0	2.50
s.e.d.		9.4***	38.9*	28.7***	1.79***	352.4**	32.6	2.14	0.912
Control	4	312.8	1667.5	664.7	102.3	1630.0	276.7	46.5	6.50
SBP <sub>60</sub> 36kg	4	520.5	1591.5	1235.3	151.5	3113.0	221.5	42.0	3.75
s.e.d.		26.5***	155.0	113.3**	8.1**	328.5**	37.7	2.63	0.382***
Control	4	652.2	1950.0	1260.0	180.0	2570.0	907.7	75.3	11.0
SBP <sub>80</sub> 108kg	12	1070.0	2197.0	2429.0	259.4	7673.0	737.2	64.9	6.9
s.e.d.		78.4***	190.6	196.1***	24.8**	690.6***	154.6	4.60*	1.52*

#### 5.4.4 THE EFFECT OF PREVIOUS NUTRITION ON FOOD INTAKE

Figure 5.2 shows the effect of previous nutrition on the food intake of pigs fed  $SBP_{80}$  at 108kg. Initially pigs with prior experience of a bulky food (T7 and T8) were able to consume significantly more of  $SBP_{80}$  than pigs previously fed C (T5). On first being given  $SBP_{80}$  the pigs previously fed  $SBP_{60}$ , either from 36 or 72kg, were able to consume 2.5 times more food than those from C. During the period the amount of  $SBP_{80}$  consumed by these pigs increased little, whereas the pigs from C, with no prior experience of a bulky food, increased their intake rapidly throughout the whole of the period. It was only after about 19 days that the intake of the pigs from C was comparable to those which had had prior experience of a bulky food.

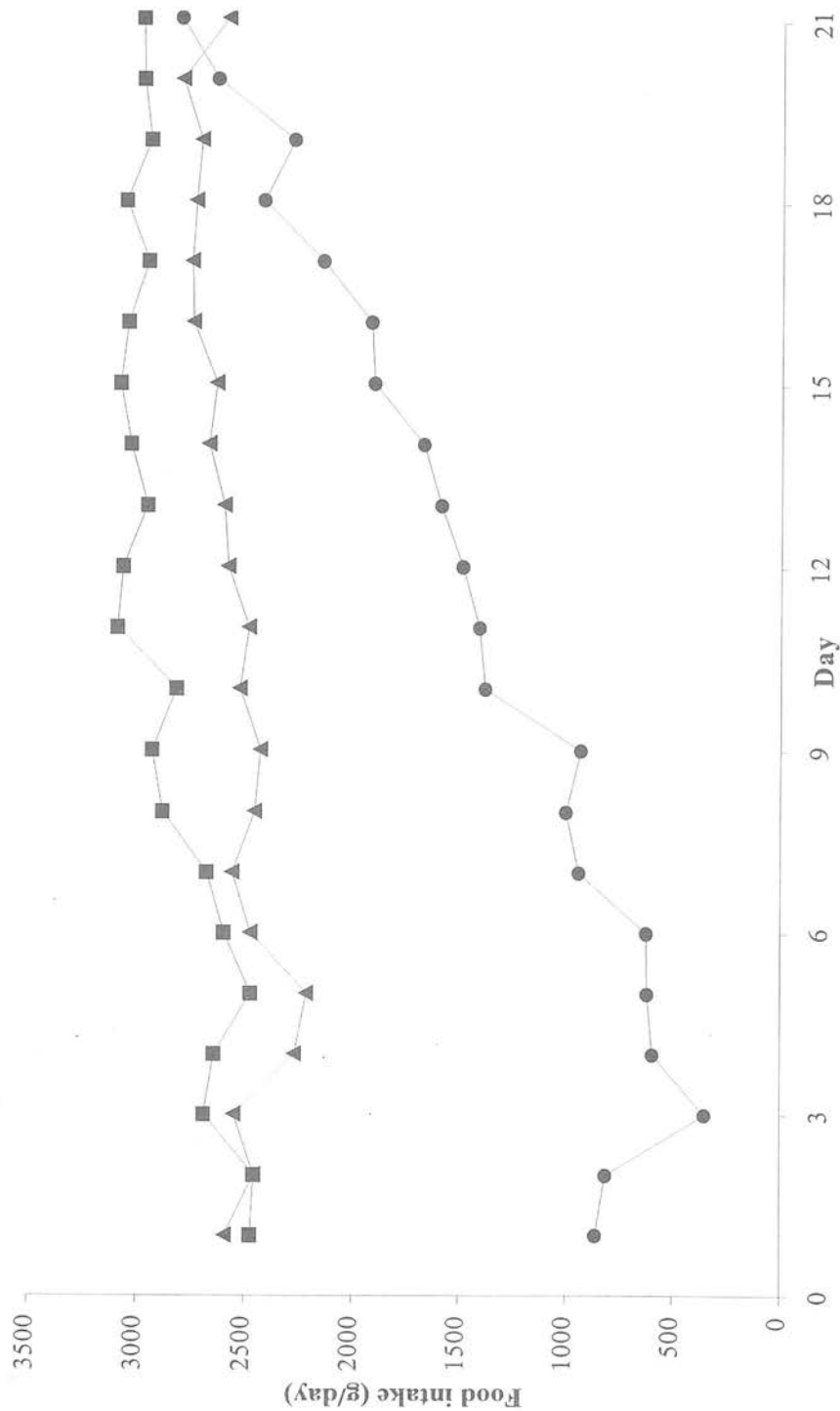


Figure 5.2. Food intake of pigs fed an 80% sugar beet pulp food (SBP80) for a period of 21 days.  $\bullet$ —, pigs fed a control food from 12–108kg and then SBP80 for period of 21 days,  $\blacksquare$ — pigs fed a 60% sugar beet pulp (SBP60) from 36–108kg and then SBP80 from 108kg for a period of 21 days,  $\blacktriangle$ — pigs fed SBP60 from 72–108kg and then SBP80 from 108kg for a period of 21 days.

#### 5.4.5 THE RELATIONSHIP BETWEEN FOOD INTAKE AND LIVEWEIGHT

Figure 5.3 shows how the scaled capacity for bulk changed with liveweight. The 4 pigs at 20kg on SBP<sub>60</sub> showed a much higher level of variation in their scaled capacity for bulk than those at other weights or that seen in previous work (Tsaras *et al.*, 1998; Chapter 2 and 3).

Despite this it is clear from Figure 5.3 that scaled capacity for bulk decreased with liveweight. The scaled capacity for bulk at 80kg, 0.178 units kg<sup>-1</sup> day<sup>-1</sup>, was significantly less than at 45kg, 0.236 units kg<sup>-1</sup> day<sup>-1</sup> (s.e.d. 0.0180,  $P < 0.01$ ), but there was no significant difference in the scaled capacity for bulk between 80 and 120kg (0.178 and 0.188 units kg<sup>-1</sup> day<sup>-1</sup> respectively, s.e.d.0.0192).

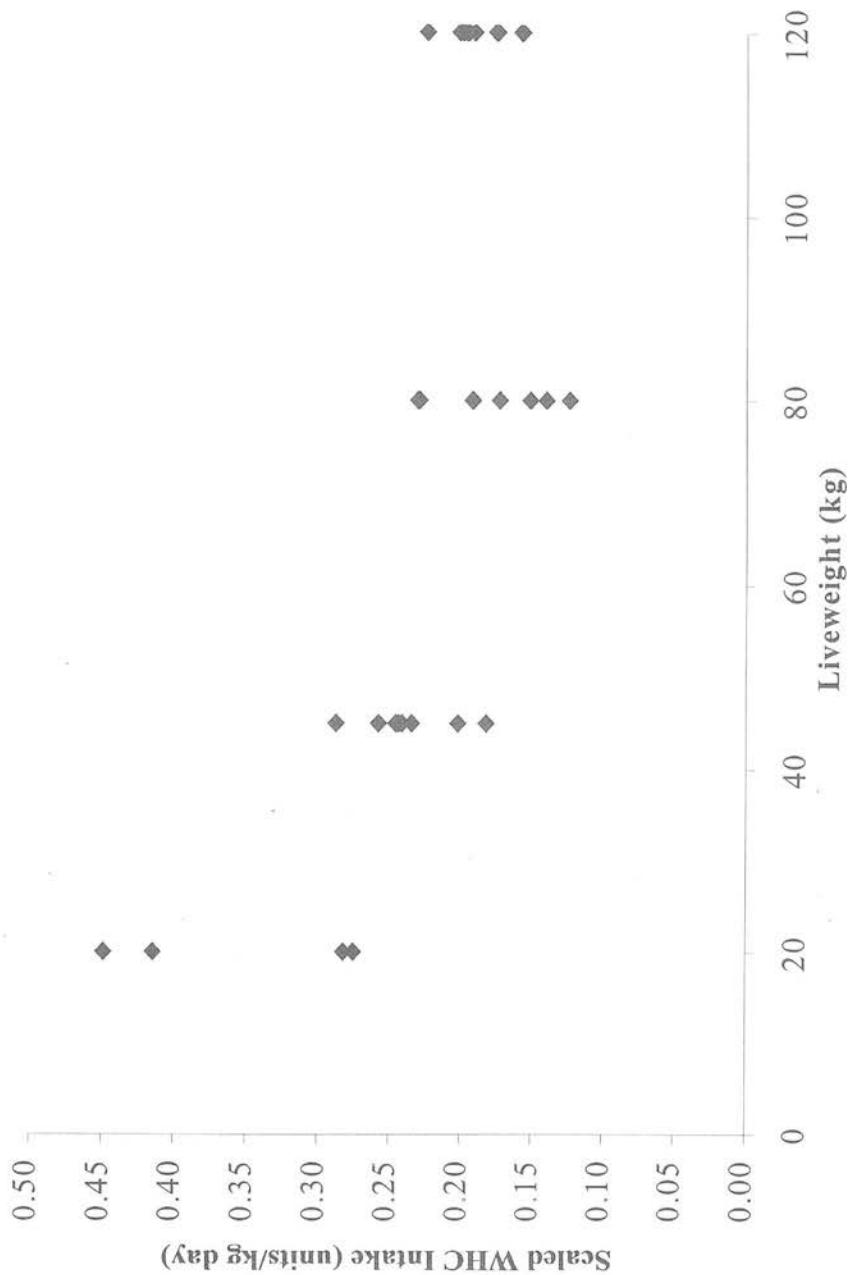


Figure 5.3. The relationship between liveweight and scaled capacity for bulk (capacity for bulk  $\text{kg}^{-1} \text{day}^{-1}$ ). Each  $\blacklozenge$  is the data from one pig. Pigs were fed a 60% sugar beet pulp food at 12, 36 and 72kg, and an 80% sugar beet pulp food at 108kg. The data are the average for the last seven days of a 21-day period.

#### 5.4.6 CHANGES IN THE SIZE OF THE GIT WITH WEIGHT

Table 5.5 shows the weight of the sections of the GIT scaled to liveweight for the pigs fed C and the pigs fed the SBP foods. For pigs fed C there was no difference in the relative weights of either the stomach or the small intestine at either 12 or 36kg, but there was a significant reduction between 36 and 108kg ( $P < 0.01$ ). The relative weights of the large intestine and the caecum increased between 12 and 36 kg ( $P < 0.05$ ) and then decreased between 36 and 108kg ( $P < 0.01$ ). Gut fill as a proportion of body weight was systematically reduced with an increase in liveweight.

On the SBP foods, the relative weights of the small intestine and gut fill declined with increasing maturity. There was no difference in the relative weights of the large intestine, the caecum, or the stomach between 12 and 36kg but there was a significant reduction between 36 and 108kg ( $P < 0.01$  and  $P < 0.001$  respectively). In general there was a bigger reduction in the proportionate weight of the GIT between 36 and 108kg than between 12 and 36kg. In contrast to this there was a significant reduction in gut fill as a proportion of body weight between 12 and 36kg ( $P < 0.01$ ), but no significant difference in gut fill, as a proportion of body weight, between 36 and 108kg.



**Table 5.5** The weights of the gastrointestinal tract sections and gut fill scaled to liveweight (LW) for pigs given access to one of three foods differing in sugar beet pulp content (control, 60% sugar beet pulp (SBP<sub>60</sub>) and 80% sugar beet pulp (SBP<sub>80</sub>)) at 12, 36 or 108kg

Treatment	N	Stomach : LW (g kg <sup>-1</sup> )	S.I : LW (g kg <sup>-1</sup> )	Large intestine: LW (g kg <sup>-1</sup> )	Caecum : LW (g kg <sup>-1</sup> )	Gut fill : LW (g kg <sup>-1</sup> )
Control 12kg	4	6.00	36.2	11.7	0.998	40.3
Control 36kg	4	6.70	35.9	14.2	2.20	34.8
Control 108kg	4	5.30	15.9	10.2	1.46	20.7
s.e.d.		0.453*	1.81***	1.23*	0.145***	5.68*
SBP <sub>60</sub> 12kg	4	10.7	39.0	23.4	2.90	115.9
SBP <sub>60</sub> 36kg	4	11.0	33.8	26.2	3.20	65.9
SBP <sub>80</sub> 108kg	12	8.9	18.2	20.2	2.15	63.6
s.e.d.		0.655**	2.03***	0.998**	0.212***	5.09***

## **5.5 DISCUSSION**

Kyriazakis and Emmans (1995), Tsaras *et al.* (1998) and Chapter 2 developed predictive relationships between food bulk and food intake that applied to young growing pigs between 12 and 40kg. This experiment was designed mainly to determine how capacity for bulk changes with increasing maturity. Data from pigs weighing more than 40kg were used to test the simple rule of Kyriazakis and Emmans (1995), that the capacity for bulk was directly proportional to weight could be extended to heavier weights. The two necessary conditions were that the high bulk foods should be limiting, and that equilibrium intake was achieved. The effects of food composition and weight on the GIT and body composition are discussed first.

### **5.5.1 THE EFFECT OF BULKY FOODS ON THE SIZE OF THE GIT AND BODY COMPOSITION**

The effects of food bulk on the GIT agreed with previous work (Stanogias and Pearce, 1985; Kyriazakis and Emmans, 1995; Jorgensen *et al.*, 1996; Pluske *et al.*, 1998; McDonald *et al.*, 2001). The weights of the stomach, the large intestine and the caecum, as well as gut fill, were increased on SBP<sub>60</sub> and SBP<sub>80</sub> compared to C. These changes are likely to reflect the parts of the gut involved in fibre digestion (Kyriazakis and Emmans, 1995). The less expected increase in stomach weight is in agreement with Jorgensen *et al.* (1996) and Houdijk *et al.* (2002).

The reductions in backfat depth seen here, although not always significant, were substantial responses to a relatively short period of feeding high fibre feeds. The effect agrees with Cole *et al.*, (1972) and Stebbens (1988) who found that the continuous feeding of high fibre foods reduced body fatness. In contrast, Kennelly and Aherne (1980), Whittaker *et al.*, (2000) and Yin *et al.* (2001) found no effect of food bulk on fat depth, while Wiseman *et al.* (1999) found that the feeding of sugar

beet pulp significantly increased carcass fatness. The fat content of the gain will reflect the ratio of the first limiting nutrient to energy where that nutrient is limiting (Kyriazakis and Emmans, 1992a and b). In some of the above experiments the addition of food bulk (fibre) to the foods could have altered this ratio and the effects on the fat content of the gain may reflect this. In our experiment the foods were formulated so that the ratio of the first limiting nutrient to energy was close to constant across the three foods, so that the effect on the fat content of the gain seen to occur here probably reflected a reduction in energy intake.

### 5.5.2 THE EFFECT OF PREVIOUS NUTRITION ON INTAKE

The pigs changed from C to SBP<sub>80</sub> initially coped much worse with the change, than did the pigs changed from SBP<sub>60</sub> (Figure 5.2) where this had been fed either from 36 or 72 kg. There was no difference between the two latter groups (Figure 5.2). By the end of the 21-day feeding period intake of SBP<sub>80</sub> was similar for pigs with the three different histories (Figure 5.2). These results agree with those found in other work on younger pigs (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998; Chapter 3).

### 5.5.3 WAS EQUILIBRIUM INTAKE ACHIEVED?

On high bulk foods that are limiting the equilibrium intake reflects the maximum capacity for that food, and it is this intake that needs to be used in predictive equations (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). It was important, therefore, that during this experiment equilibrium intakes were achieved. The period of 21 days on the high bulk foods was intended to provide 14 days for adaptation (Owen and Ridgman, 1968; Kyriazakis and Emmans, 1995; Chapter 2) and then a 7-day period during which equilibrium food intake could be recorded. For pigs changed from C to SBP<sub>60</sub>, at 12 (T1) or 36kg (T3), a period of 14 days proved to be

long enough to allow the pigs to become fully adapted to the new food. An equilibrium intake was achieved in the third week as judged by Figure 5.1. However, it was clear that the pigs of 108kg coming from C did not achieve an equilibrium intake on SBP<sub>80</sub> (T5) within 14 days (Figure 5.1). The pigs on this treatment took 19 days to adapt to the food they were on (Figures 5.1, 5.2) indicating that adaptation takes longer in the pigs fed SBP<sub>80</sub> at 108kg.

It is not clear if the increased adaptation time in the pigs fed SBP<sub>80</sub> at 108kg is the result of the pigs being older rather than being due to the increased SBP content of the food used. However, Tsaras *et al.* (1998) found that a period of 14 days was long enough for pigs between 12 and 40kg to adapt to a food containing 800g kg<sup>-1</sup> sugar beet pulp. It therefore seems more likely that the longer period needed for adaptation is because the pigs are heavier. The slower adaptation in pigs changed from C to SBP<sub>80</sub> at 108kg may be because the GIT becomes less able to adapt to high bulk foods with increasing weight.

Although the pigs changed from C to SBP<sub>80</sub> at 108kg did not achieve equilibrium intake during the last 7 days of the period, it was shown that the pigs changed from SBP<sub>60</sub> to SBP<sub>80</sub> at 108kg (T7 and T8) did achieve equilibrium intake. Estimates of equilibrium intake at the heaviest weights used were thus achieved.

#### **5.5.4 WERE THE HIGH BULK FOODS CONSTRAINING?**

It was expected that a food containing 600g kg<sup>-1</sup> sugar beet pulp would be limiting for pigs in the weight range of 12 – 40kg (Tsaras *et al.*, 1998; Chapter 3). This level of SBP may not have limited the performance of pigs weighing 108kg (Owen and Ridgman, 1967; Kenelly and Aherne, 1980; Wenk, 2001) due to the increased size of their GIT and so a food containing 800g kg<sup>-1</sup> sugar beet pulp was used at this weight. Using more than 800g kg<sup>-1</sup> sugar beet pulp to the diet was not possible because the

foods were formulated to have similar calculated ratios of protein, amino acids, vitamins and minerals to DE.

To determine if a food was constraining the adapted performance of the pigs fed the SBP foods was compared with that achieved by pigs fed the control food at the same weight (Table 5.3). The results clearly show that a 60% sugar beet pulp food was limiting when fed to pigs at 12kg. However, the high SBP foods could not be shown to be limiting performance at 36, 72kg or 108kg. This had not been expected.

The effects of an increase in gut fill may in part, explain the high levels of gain in liveweight achieved on SBP<sub>60</sub> and SBP<sub>80</sub>. Pigs fed the high bulk foods had between 2 and 3 times as much gut fill as those fed C (Table 5.4) at the same weight. The results after accounting for gut fill effects (see Materials and methods) are in Table 5.6. On the high SBP foods the adjusted liveweight gain (aLWG) was 0.728 at 12kg, 0.889 at 36 kg, 0.831 at 72 kg and 0.824 at 108 kg of that on C. Although the reductions were large it was only at 12 kg that the difference was formally significant. The consistency of the reduction strongly indicates that the foods used were limiting and hence that the data can be used to determine the maximum capacity for bulk at a given weight.

**Table 5.6.** The means for absolute liveweight gain (LWG, for the last 7 days before slaughter), rate of change in food intake (for the last 7 days before slaughter), gut fill (on the day of slaughter), rate of change in gut fill and LWG adjusted for gut fill of pigs given access to one of three foods differing in sugar beet pulp content (control, 60% sugar beet pulp (SBP<sub>60</sub>) and 80% sugar beet pulp (SBP<sub>80</sub>)) at 12, 36 or 108kg

Treatment	N	LWG (g day <sup>-1</sup> )	Rate of change in food intake (g day <sup>-2</sup> )	Gut fill (g g food <sup>-1</sup> )	Rate of change in gut fill (g day <sup>-2</sup> )	LWG adjusted for gut fill (g day <sup>-1</sup> )	FCE
Control	26	743	51.8	0.870	47.2	691	0.720
SBP <sub>60</sub> 12kg	4	608	52.5	2.00	105.3	503	0.413
s.e.d.		40.8**	19.8	0.184***	37.4**	41.6***	0.0782***
Control	16	892	97.5	0.837	79.2	813	0.449
SBP <sub>60</sub> 36kg	8	760	21.9	1.83	37.7	723	0.427
s.e.d.		98.6	21.7*	0.255**	20.1	74.8	0.0221
Control	8	1103	38.9	0.854 <sup>†</sup>	33.2 <sup>†</sup>	1070 <sup>†</sup>	0.444
SBP <sub>60</sub> 72kg	8	997	56.2	1.92 <sup>†</sup>	107.9 <sup>†</sup>	889 <sup>†</sup>	0.387
s.e.d.		96.0	18.4				
Control	4	1012	68.7	0.813	53.7	958	0.305
SBP <sub>80</sub> 108kg	12	947	54.7	2.85	158.0	789	0.282
s.e.d.		135.4	26.9	0.349***	75.2	129.2	0.0431

<sup>†</sup> estimated using the gut fill data from 12, 36 and 108kg.

### 5.5.5 THE RELATIONSHIP BETWEEN FOOD INTAKE AND LIVWEIGHT

The way in which the intake of WHC per kg changed with weight was presented in Figure 5.3. From this, and from the formal analysis of the results in Table 5.3, it is clear that the capacity scaled directly to weight is not constant across the range of weights used. Figure 5.4 shows the way in which the absolute capacity for bulk changed with liveweight, both a quadratic and a linear function have been fitted to the data. The relationship between the absolute capacity for bulk (Cap) and liveweight (W) was best described by the quadratic function:

$$\text{Cap} = (0.238.W) - (0.000466.W^2) \quad \text{units day}^{-1} \text{ (rsd 2.60)} \quad (1) \\ (\text{s.e. } 0.02527) \quad (\text{s.e. } 0.0002405)$$

The above quadratic function predicts that the capacity per kg will decrease as weight increases. This shows that the approximate rule of proportionality suggested by Kyriazakis and Emmans (1995) does not hold across the whole relevant weight range. The absolute capacity is predicted to reach a maximum when  $W = 255\text{kg}$ , a value that approximates to the mature weight suggested by Knap (2000).

Scaled capacity for bulk will be a directly proportional to liveweight (as suggested by Kyriazakis and Emmans, 1995) only when the relationship between capacity for bulk and liveweight is linear. The linear function shown in Figure 5.4 is

$$\text{Cap} = 0.190W \quad \text{units day}^{-1} \text{ (rsd 2.77)} \quad (2) \\ (\text{s.e. } 0.005917)$$

The quadratic function provided a significantly better fit to the data than the linear one ( $P < 0.05$ ). Therefore the idea that capacity for bulk is directly proportional to liveweight across the whole relevant weight range can be rejected. For both the linear and the quadratic function the intercept is forced to be zero. This has the nice mathematical consequence that only two, not three, parameters need to be estimated, it also has the advantage that an animal weighing 0kg will have a food intake of zero.

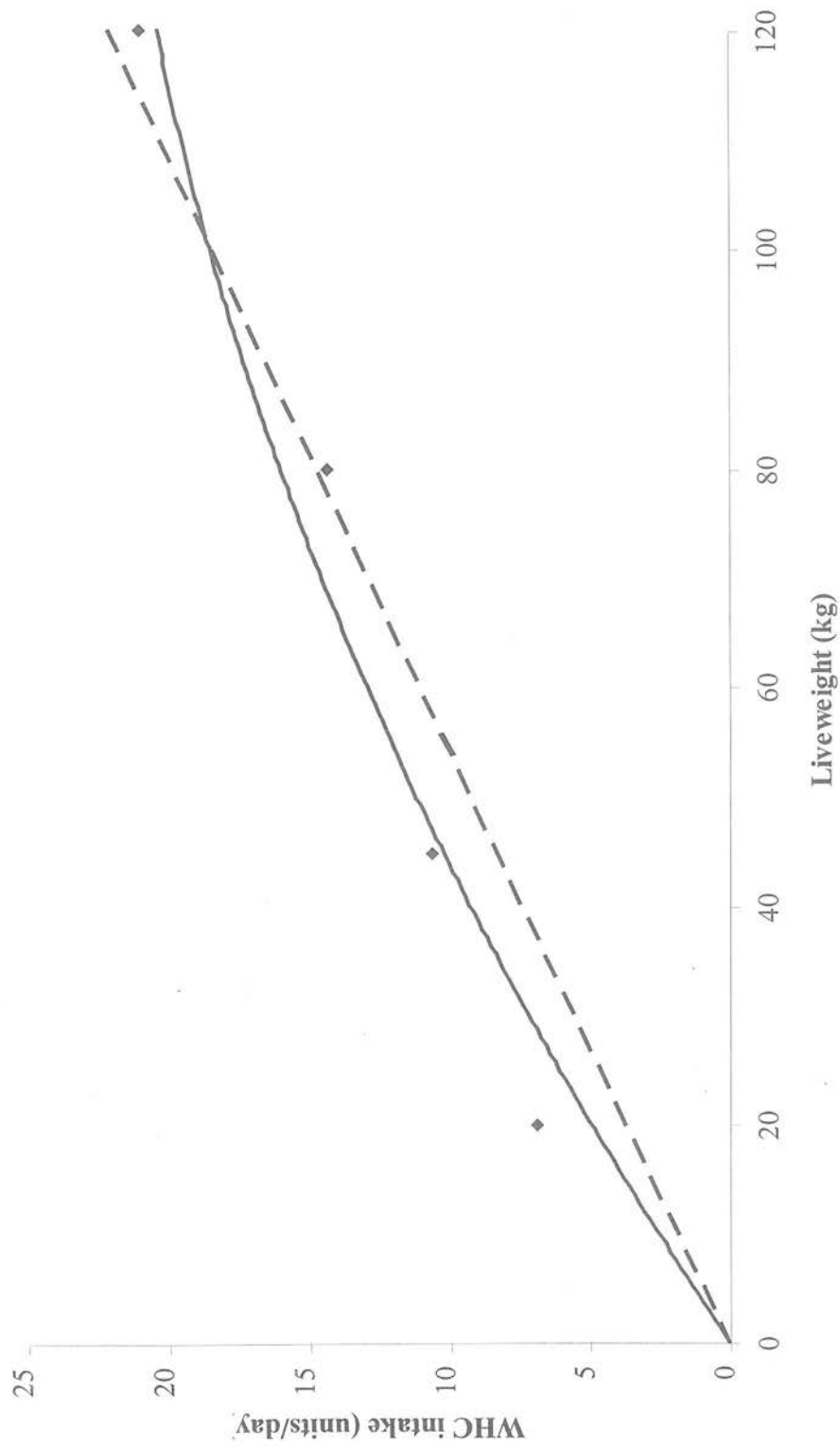


Figure 5.4. The relationship between absolute capacity for bulk and liveweight. The solid line is that fitted by the equation  $y = (0.262.x) - (0.000767.x^2)$  and the dotted line is that fitted by the equation  $y = 0.184x$ .



The equations given above use all the data collected during the experiment, however, in comparison with previous work (Tsaras *et al.* 1998; Chapter 2 and 3), it would seem that the food intake achieved on SBP<sub>60</sub> at 12kg (Table 5.3) was much higher than expected. We have no explanation for this. The results of Tsaras *et al.* (1998) and Chapter 2 show a scaled food intake on a 58% sugar beet pulp food in 20kg pigs of 43g kg<sup>-1</sup> day<sup>-1</sup> compared to the much higher value in Table 5.3 of 57.0g kg<sup>-1</sup> day<sup>-1</sup>. It would seem that there were two pigs with high and deviant intakes (see Figure 5.3) that were responsible. Therefore, in Figure 5.5 the value used at the lowest weight is taken from the literature (Tsaras *et al.* 1998; Chapter 2 and 3), is based on the data from 40 animals, and is seen as being more reliable. To ensure that the data taken from the literature was comparable with that collected during this experiment, the WHC values of the foods used in the literature were re-estimated using the WHC data collected in the current experiment.

The new relationship between the absolute capacity for bulk (Cap) and liveweight (W) shown in Figure 5.5 was described by the quadratic function:

$$\text{Cap} = (0.230.W) - (0.000476.W^2) \quad \text{units day}^{-1} \quad (\text{rsd } 1.19) \quad (3)$$

(s.e. 0.03007) (s.e. 0.0002883)

The above relationship describes the data well. The value of the constants in the above equation are not greatly different to those in equation (1), however the above equation gives an improved rsd (1.19 v's 2.60 respectively).

The above function predicts that the capacity per kg will decrease as weight increases. It is predicted to be 0.224 at 12kg, 0.213 at 36kg, 0.196 at 72kg and 0.179 at 108kg. It is thus predicted to be virtually constant between 12 and 36kg in agreement with the results and analyses of Kyriazakis and Emmans (1995), and Chapter 2. Again it is clear that this approximate rule does not hold across the whole relevant weight range. A decline in the rate of increase in absolute capacity for bulk with an increase in weight is in agreement with the results of work done in growing

sheep (Emmans and Friggens, 1995). The absolute capacity is predicted to reach a maximum when  $W = 242\text{kg}$ , a gain this is a value not far away from a likely mature weight (Knap, 2000).

An alternative form of function to relate Cap to  $W$  is an exponential one:

$$\text{Cap} = 42.1(1 - e^{-0.00564W}) \quad \text{units day}^{-1} \quad (\text{rsd } 1.16) \quad (4)$$

(s.e. 19.3)      (s.e. 0.00338)

where 42.1, is an estimate of the maximum and  $W$  is weight. The function predicts that there will be a curvilinear increase in Cap with an increase in liveweight until a maximum is reached. Unlike the quadratic function the exponential relationship does not predict that capacity for bulk will begin to decline above a weight of 242kg. Over the weight range of interest the exponential function is no more accurate than the quadratic function as shown by the rsd's.

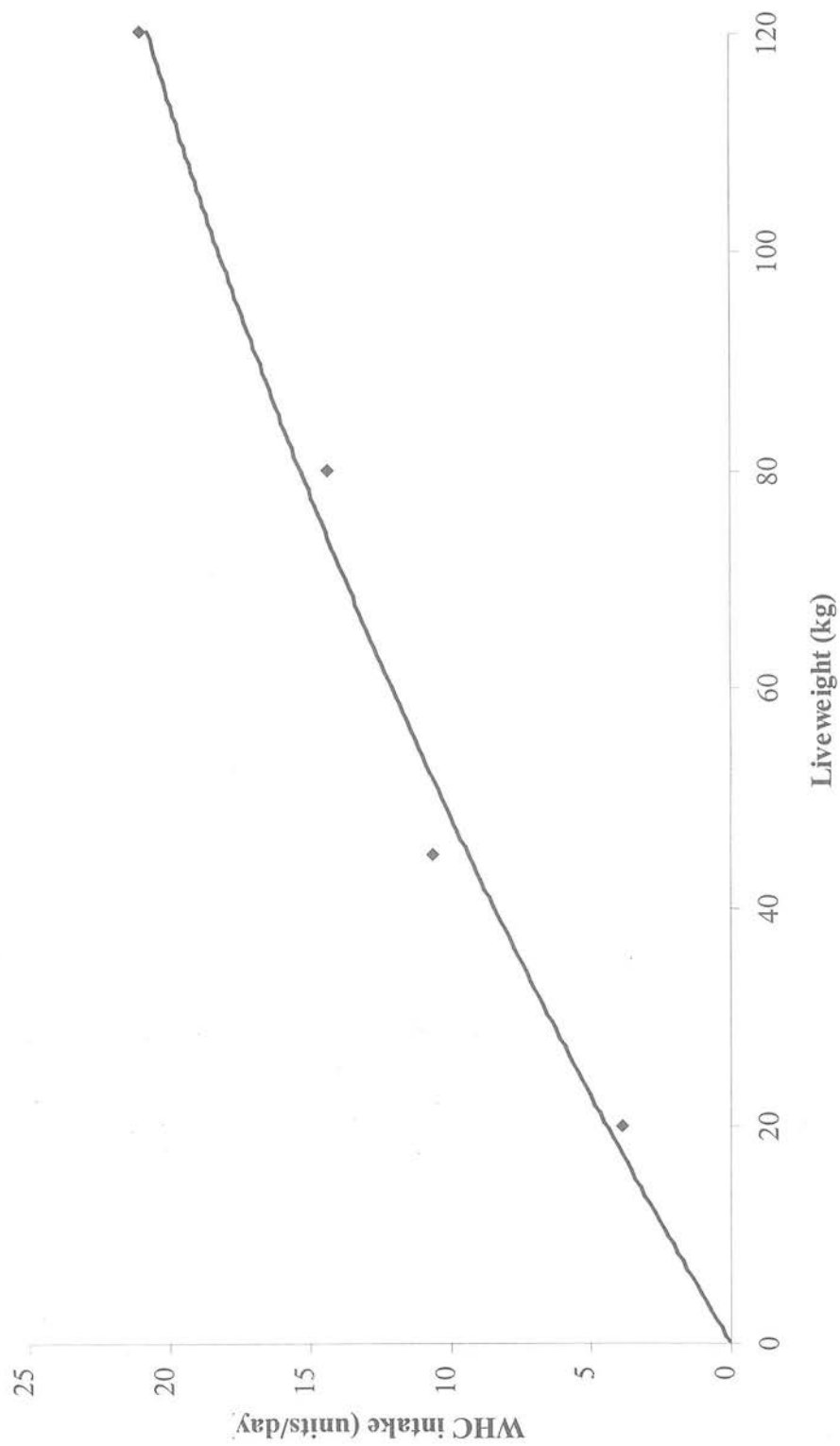
The decrease in the scaled capacity for bulk with weight is consistent with the fact that, in general, the weight of the components of the GIT and gut fill relative to body weight also declined between 12kg and 108kg (Table 5.6). The weights of the large intestine and the caecum, as proportions of body weight, were not reduced between 12 and 36kg, which is also consistent with virtually no reduction in the scaled capacity for bulk between these two weights. The capacity for food bulk is likely to be linked to the size of the gastrointestinal tract. In particular the large intestine and caecum, which are the main sites of fibre digestion (Stanogias and Pearce, 1985; Varel, 1987; Kyriazakis and Emmans, 1995; Pluske *et al.*, 1998), may be important. If the size of the large intestine (LI) and the caecum are important for the control of intake on bulky foods, changes in capacity for bulk with increasing liveweight might be expected to mirror changes in the size of the LI and the caecum with increasing liveweight. Figure 5.6 shows how the capacity for bulk and the combined weight of the LI and caecum changed in the same way with increasing liveweight. The quadratic function

$$\text{WLIC} = 0.0344.W - 0.0000998.W^2 \quad \text{kg (rsd 0.0794)} \quad (5)$$

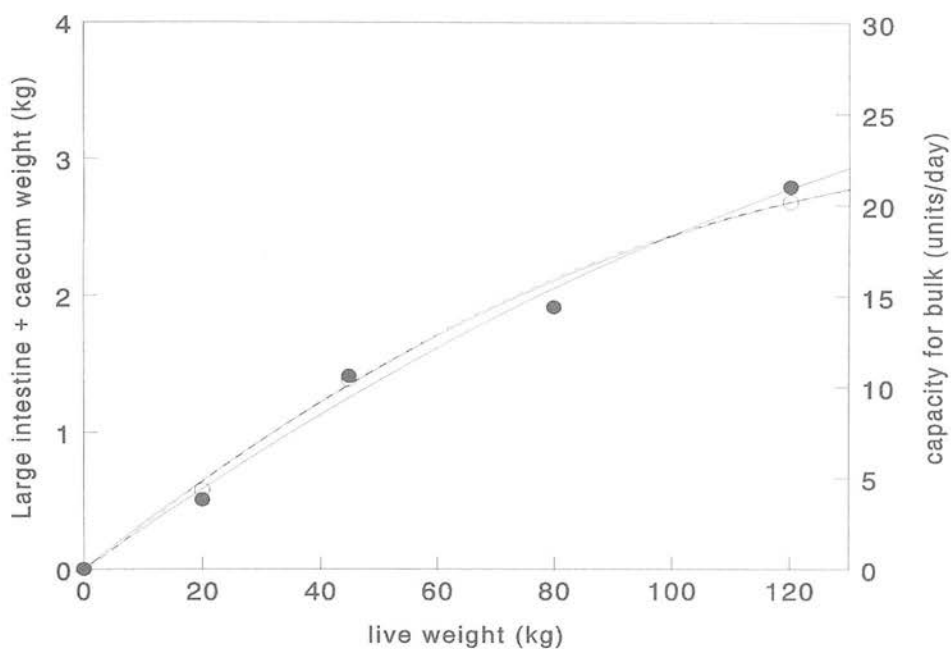
(s.e. 0.00245) (s.e. 0.0000218)

where WLIC is the combined weight of the LI and the caecum and W is the liveweight provided an accurate description of the relationship between the combined weight of the LI and the caecum and liveweight. This function predicts that the combined relative weight of the LI and caecum ( $\text{g kg}^{-1} \text{ day}^{-1}$ ) will be 33.2 at 12kg, 30.8 at 36kg and 23.6 at 108kg. These are consistent with the changes in scaled capacity for bulk with an increase in liveweight. Although, weight may not be an entirely appropriate measurement of capacity, Figure 5.6 does provides some evidence that there is a link between the size of the LI and the caecum and the capacity to consume food bulk.

The predicted values from equations 2 and 4 show that the ratio of Cap divided by WLIC varied little around a mean value of seven across the weight range of interest. This suggests that the size of that WLIC could well determine Cap.



**Figure 5.5** The relationship between absolute capacity for bulk and liveweight. The data at 20kg was estimated from the data of Tsaras et al. (1998) and Chapters 2 and 3.



**Figure 5.6.** The relationship between capacity for bulk and liveweight (●) and the relationship between large intestine + caecum weight and liveweight (○). The solid black line is that fitted by the equation  $y = 0.230x - 0.000476x^2$ , and the broken line is that fitted by the equation  $y = 0.0344x - 0.000998x^2$ .

## **5.6 CONCLUSIONS**

Knowledge of the animal's capacity for bulk and of the WHC of the food allows constrained food intake (CFI) to be predicted, as CFI is a function of an animal's capacity to consume food bulk and the bulk content of the food. The original rule that made constrained food intake proportional to liveweight was found not to apply over the whole relevant weight range. A quadratic regression was found to provide an accurate description of the relationship between liveweight and capacity for bulk. The way in which the weights of the large intestine and caecum changed with liveweight was similar to the way in which Cap changed with liveweight. This provides some evidence that there is a link between the weight of the large intestine and the caecum and capacity for food bulk.

# **CHAPTER 6**

**The problem of predicting food  
intake during the period of  
adaptation to a new food: a model.**

## 6.1 ABSTRACT

A model is described which aims to predict intake immediately following a change from one food to another that is higher in bulk content; it deals with the transition from one 'equilibrium' intake to another. The system considered is an immature pig fed *ad libitum* on a single homogenous food, which is balanced for nutrients and contains no toxins so that the first limiting resource is always energy. It is assumed that an animal has a desired rate of intake (DFI) which is that needed to meet the energy requirements for protein and lipid deposition and for maintenance. DFI may not be achieved if a bulk constraint to intake exists. Where a bulk constraint operates intake is calculated as constrained intake (CFI) where  $CFI = C_{whc}/WHC \text{ kg day}^{-1}$ , WHC is the water holding capacity of the food (kg water/kg dry food) and  $C_{whc}$  is the animal's capacity for WHC (units/kg liveweight day). Where intake is not constrained it is assumed that genetic potential will be achieved. Potential growth rate is described by the Gompertz growth function. Where intake is constrained, growth will be less than the potential. Constrained growth rate is predicted as  $(dW/dt)_{con} = (EI - E_m)/e_g \text{ kg day}^{-1}$  where EI is energy intake ( $\text{MJ day}^{-1}$ ),  $E_m$  is the energy required for maintenance ( $\text{MJ day}^{-1}$ ) and  $e_g$  is the energy required for unit gain ( $\text{MJ kg}^{-1}$ ). The value of  $e_g$  depends on weight and the fattening characteristics of the pig. Actual growth is predicted to be the lesser of potential and constrained growth. To deal with adaptation it is assumed that the time taken to reach equilibrium depends on the difference in WHC values between the previous and current food and that the capacity to consume food bulk is related to the WHC of the current food. It is proposed that the capacity for WHC on the first day on a new food will be equal to the current capacity for WHC on the last day of the previous food so that  $C_{whc} = (FI \cdot WHC)/W \text{ g kg}^{-1}$ , where FI is food intake ( $\text{kg day}^{-1}$ ), and W is pig weight (kg). Thereafter  $C_{whc}$  will gradually increase over time to a maximum of  $0.27 \text{ g kg}^{-1}$ . The rate of change in  $C_{whc}$  is made to be the same for all pigs and all foods. The increase in capacity over time is assumed to be linear at the rate of  $0.01 \text{ units/day}$ . The model was parameterised using data collected from pigs in the weight range of 12 - 45kg



and was tested using published data. Qualitatively the predictions of the model were in close agreement with the relevant observed data in at least some cases. It is concluded that the underlying theoretical assumptions of the model are reasonable. However, the model fails to predict initial intake when changed to foods high in wheatbran content and fails to predict the intake of a non-limiting food where compensatory increases in intake and gain occur. The model could be adapted to overcome the first failure by taking into account the time course of digestive efficiency following a change in food. To deal with the second would require a sufficient understanding of the time course of compensatory growth.

## **6.2 INTRODUCTION**

Some current models of food intake seek to predict the way in which the intake of a given food will change over time (Black *et al.*, 1986; Ferguson *et al.*, 1994; Kyriazakis and Emmans, 1995; Emmans, 1997; Giles *et al.*, 1998; Kyriazakis and Emmans, 1999; Whittemore *et al.*, 2001). These models assume that the animal is always fully adapted to the food it is on, i.e. equilibrium with the food is presumed. This approach, however, does not account for the immediate effects of a change in food type upon intake. A change in food type may have important consequences for both food intake and performance, particularly when the change is from one food to another of poorer nutritional quality (e.g. Kyriazakis and Emmans, 1995; Chapter 3).

Changing to a food with a greater bulk content results, initially, in a reduction in food intake and performance (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998; Chapter 3). The reduction in food intake is a reflection of the fact that the gastrointestinal tract is not adapted to the new food and is the result of the physical 'bulk' of the new food exceeding the capacity of the gastrointestinal tract for bulk (Cole *et al.*, 1972; Kyriazakis and Emmans, 1995). After the initial reduction in intake there is a transition period during which intake gradually increases until the new equilibrium intake is reached. This is determined by the 'bulk' content of the food and the capacity of the gastrointestinal tract for bulk (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). Adaptation involves accommodation of the gastrointestinal tract to the increased gut fill or to the increased involvement of parts of the gut in fibre digestion (Kyriazakis and Emmans, 1995). The increase in intake over time, during this period of adaptation, is the result of an increase in the weight (size) and volume of the gastrointestinal tract, particularly of the large intestine (Low, 1985; Kyriazakis and Emmans, 1995). The length of the adaptation period, and the extent to which food intake is initially reduced after a change in food type, have both been shown to be related to the difference in bulk content between the two foods (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998; Chapter 3). Previous nutritional history will

have significant effects on adaptation. For example, animals that have had previous experience of bulky foods show an enhanced capacity for bulk. In chapter 3 it was found that pigs with previous experience of bulky foods were able to consume up to 1.4 times as much of a high bulk food than pigs that had previously been fed a low bulk food. Kyriazakis and Emmans (1995) showed that previous experience of bulky foods led to a reduction in the time taken to adapt to a bulky food and to an increase in food intake.

The adaptation period has important implications for the intake and performance of pigs fed high bulk foods. It is during this time that food intake and performance will be depressed to the greatest extent and it may take up to 14 days for an animal to become fully adapted to a new food which is high in bulk (Kyriazakis and Emmans, 1995). The ability to predict the extent to which intake and performance will be depressed, and for how long the period of adaptation will last after a change in food type, will allow more accurate food intake prediction models for high bulk foods to be developed, and may help to develop feeding strategies that will minimise the effects of adaptation. Despite this, data recorded during the period of adaptation are frequently excluded in order to make the prediction of food intake on high bulk foods easier (e.g. Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). The aim of this work is to develop a model that will predict intake and performance during the transition period between equilibrium intakes when the animal is changed from one food type to another that is higher in bulk content. The approach is expected to complement existing models that predict the food intake of pigs.

## **6.3 MATERIALS AND METHODS**

### **6.3.1 DESCRIPTION OF THE MODEL**

#### ***6.3.1.1 GENERAL***

The system being considered is an immature pig fed *ad libitum* on a single, homogenous food that is balanced for nutrients and contains no toxins, so that the first limiting resource is always energy. The environment is always maintained at thermoneutrality. For the purposes of the model, it is assumed that the pig eats to attain its genetic potential for performance subject only to the presence of constraints (Emmans 1988; 1997; Black *et al.*, 1986; Ferguson *et al.*, 1994, Poppi *et al.*, 1994 and Kyriazakis and Emmans 1999). According to this framework animals are assumed to have a desired food intake (DFI) which is determined by the genetic potential for protein deposition, the desired rate of lipid deposition, and by the current requirement for maintenance (Kyriazakis and Emmans, 1999). In a thermally neutral environment, it is only these 'goals' that determine the rate of food intake needed to meet the requirement for energy. It is possible that constraints arising from the food being offered may prevent DFI from being met. The only constraint to food intake considered here is the bulk content of the food. Where a bulk constraint operates, actual food intake is predicted to be less than desired food intake and hence genetic potential is not achieved. Where a bulk constraint operates, actual food intake is calculated as constrained food intake (CFI). CFI is a function of the bulk content of the food and the capacity of the pig to deal with that bulk (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998, Kyriazakis and Emmans, 1999). The bulk content of a food is measured by its water holding capacity (WHC), which is a measure a material's ability to hold water within its matrix and has been shown to be a good indicator of food bulk (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998).

The theoretical assumptions laid out above form the basis of the model, the aim of which is to predict food intake and performance during the transitory period when a

change in food type from one food to another of a higher bulk content occurs. There were several stages of model development. The first step was to predict equilibrium food intake as a function of the animal's current state. Next the model was made dynamic, so that changes in equilibrium intake and performance over time could be predicted. For this purpose, the rate of change of state as weight gain was made a function of genotype, current state and predicted intake (Emmans, 1997). The third stage was to make the model able to deal with the transitory period when a change in food type from one food to another of higher bulk content occurs. It was assumed that the time taken to reach equilibrium depends on the difference in WHC between the foods. The capacity to consume food bulk is assumed to be related to the WHC of the current food (Kyriazakis and Emmans, 1995).

### **6.3.2 STATIC MODEL**

#### ***6.3.2.1 POTENTIAL GROWTH***

Where food intake is not constrained it is assumed that genetic potential, or maximal growth, can be achieved. For immature animals potential growth can be described by the Gompertz growth function (Emmans, 1988; Emmans and Kyriazakis, 1999; 2001). This approach has been successfully used for pigs by Whittemore *et al.*, (1988) and more recently by Knap (2000). Potential growth rate at a given weight is given by

$$(dW/dt)_{\max} = B.W.\log_e (A/W) \text{ kg day}^{-1} \quad (1)$$

where W is current body weight (kg), B is a rate parameter (/d) and A is mature size (kg).

### 6.3.2.2 ENERGY REQUIREMENT

Energy is the only resource that will be considered. The scale of energy used to estimate requirements is important and here the effective energy (EE) scale developed by Emmans (1994) is used. The advantages of this system have been discussed elsewhere (Emmans, 1994; 1997; Emmans and Kyriazakis, 2001). In principle, however, any other energy system (e.g. ARC, 1981; NRC, 1988; Noblet *et al.*, 1993) could be used in its place. The starting point for the effective energy system is metabolisable energy, which is corrected for the digestibility and fermentability of the diet and for its, protein and lipid contents. It is assumed that the effective energy requirements for unit gains of protein and lipid gains constant across foods and level of feeding. These requirements were also found to be constant across species and degrees of maturity (Emmans, 1994).

The requirement for EE ( $EE_{rq}$ ) by the growing animal is calculated as the sum of the requirements for maintenance (m), protein retention (pr) and lipid retention (lr) as follows

$$EE_{rq} = EE_m + EE_{rqgain} \text{ MJ day}^{-1} \quad (2)$$

where,  $EE_m$  ( $\text{MJ day}^{-1}$ ) is the effective energy required for maintenance,  $EE_{rqgain}$  ( $\text{MJ day}^{-1}$ ) is the effective energy required for potential protein and lipid growth at a given weight (see below).

The effective energy required for maintenance is assumed to be directly proportional to W and can be calculated as

$$E_m = a.W \text{ MJ day}^{-1} \quad (3)$$

Although there are good reasons for assuming that maintenance is directly related to protein weight rather than body weight (Emmans, 1987; 1994), for the purposes of

the current model the use of body weight to predict the requirements for maintenance is considered to be adequate. The aim of this part of the model is not to predict whole pig growth but rather to provide a basis from which a model to predict intake and performance during the adaptation period to bulky foods could be developed. In addition to this, body protein content is not expected to change much over the weight range of interest and hence little extra accuracy will be gained by using protein weight rather than weight.

### 6.3.2.3 PREDICTING FOOD INTAKE

Where food intake is unconstrained and maximum performance can be achieved, an animal is presumed to eat at a level that will allow its requirements to be met so that

$$DFI = RQ/FEEC \text{ kg day}^{-1} \quad (4)$$

where RQ (MJ day<sup>-1</sup>) is the requirement for energy and FEEC is the energy content of the food (MJ kg<sup>-1</sup>). As long as RQ can be predicted, and FEEC is known or can be calculated, then DFI can be predicted.

Where intake is constrained by the bulk content of the food it will be determined by the animal's capacity for bulk and the bulk content of the food so that a constrained food intake (CFI) is given by

$$CFI = C_{whc}/WHC \text{ kg day}^{-1} \quad (5)$$

Where  $C_{whc}$  (kg kg<sup>-1</sup> day<sup>-1</sup>) is the animal's maximum capacity for water holding capacity and WHC (kg kg<sup>-1</sup>) is the water holding capacity of the food. Kyriazakis and Emmans (1995) and Tsaras *et al.* (1998) found that, over the weight range 12-45kg in pigs, the capacity for bulk was directly proportional to the animal's weight (W), so that

$$C_{\text{whc}} = z.W \text{ units day}^{-1} \quad (6)$$

Actual food intake (FI) is then predicted as the lower of DFI and CFI.

Actual energy intake (EI, MJ day<sup>-1</sup>) which is used to calculate growth on a constraining food (see below) is then calculated as follows

$$EI = FI.FEEC \text{ MJ day}^{-1} \quad (7)$$

#### 6.3.2.4 PIG GROWTH ON A CONSTRAINING FOOD

On a food where intake is constrained, growth rate will be less than the potential. Weight gain on a constraining food is predicted from the following energy relationship

$$(dW/dt)_{\text{con}} = (EI - E_m)/e_g \text{ kg day}^{-1} \quad (8)$$

where  $E_m$  (MJ day<sup>-1</sup>) is the energy required for maintenance and  $e_g$  (MJ kg<sup>-1</sup>) is the energy required for unit growth. All energy values are expressed as effective energy (Emmans, 1994).

Actual growth is then predicted to be the lesser of potential  $((dW/dt)_{\text{max}})$  and constrained  $((dW/dt)_{\text{con}})$  growth.

#### 6.3.2.5 ENERGY REQUIRED FOR GAIN

For the model to work the energy required for potential growth,  $EE_{\text{rgain}}$  MJ d<sup>-1</sup>, and the energy needed per unit of constrained growth,  $e_g$  MJ kg<sup>-1</sup>, for constrained growth need to be calculated. It is assumed that energy is needed above maintenance only



for protein and lipid retention and that the composition of the gain of a given kind of pig is constant regardless of the type of food being fed. These rates of retention need to be estimated as functions of  $W$ , as this is the variable used in the model to describe pig size. A separate body composition sub-model was used to achieve this.

The sub model was set up as a spreadsheet to predict weight,  $W$ , protein weight,  $P$ , and lipid weight,  $L$ , from birth, at  $W = 1.0$  kg, to maturity for different kinds of pig. All pigs were assumed to have the same mature protein mass,  $P_m$ , of 40kg but to have different ratios of lipid to protein at maturity,  $LPR_m$  (mature lipid to protein ratio) =  $L_m/P_m$ . Values of  $P$  between 0.1 kg and  $P_m$  were set as a column in the spreadsheet. The weights of the other chemical components of the body were then calculated assuming allometric relationships (Emmans and Fisher, 1986; Emmans and Kyriazakis, 1995b). For ash (ASH), water (WA) and lipid (L) the relationships used (Emmans and Kyriazakis, 1997) were

$$ASH = k_1.P^b \text{ kg} \quad (9)$$

$$WA = k_2.P^c \text{ kg} \quad (10)$$

$$L = k_3.P^d \text{ kg} \quad (11)$$

Body weight is then calculated as the sum of  $P$ ,  $WA$ ,  $ASH$  and  $L$ . The values of the parameters for ash and the parameter  $c$  for water were assumed to be constant across pigs. The values of the water parameter  $k_2$  was made a function of the mature protein to water ratio at maturity ( $WAPR_m$ ) and the lipid parameters,  $k_3$  and  $d$ , were made functions of  $LPR_m$  as described below.

Different forms were used to describe the relationships between  $P$  and  $W$ , and  $L$  and  $W$  for each of a range of  $LPR_m$  values of 0.5, 1.0 ... 5.0. The first form used was that of the simple allometric:  $P = x_1.W^y$  and  $L = x_2.W^z$  following Whittemore *et al.* (1988). This form of function was rightly criticised by Schinckel (1999) and its use here resulted in large systematic deviations between the values predicted by the function and the input data. Schinckel (1999) suggested that an augmented allometric function

of the form  $Y = aX^b(c-X)^d$  would be better at describing the relationships between P and W and L and W. However, there is no theoretical reason for using this form rather than other simpler functional forms such as the quadratic. The form of the augmented allometric function will not, therefore, be considered further. A simple linear function described the relationships between P and W, and L and W better than the simple power function but gave deviations that were systematic and larger than were judged to be satisfactory. Deviations from a quadratic model were also systematic, but were acceptably small for the present purpose as illustrated in Figures 6.1a for protein and 6.1b for lipid. The relationships between P and W and L and W were thus estimated from:

$$P = a_1 + b_1.W + c_1.W^2 \text{ kg} \quad (12)$$

$$L = a_2 + b_2.W + c_2.W^2 \text{ kg} \quad (13)$$

From the above, the protein and lipid contents of live weight gain at a live weight become:

$$dP/dW = b_1 + 2c_1.W \text{ kg kg}^{-1} \quad (14)$$

$$dL/dW = b_2 + 2c_2.W \text{ kg kg}^{-1} \quad (15)$$

The values of the four parameters,  $b_1$ ,  $c_1$ ,  $b_2$ , and  $c_2$  were estimated for a type of pig with a particular value of  $LPR_m$ .

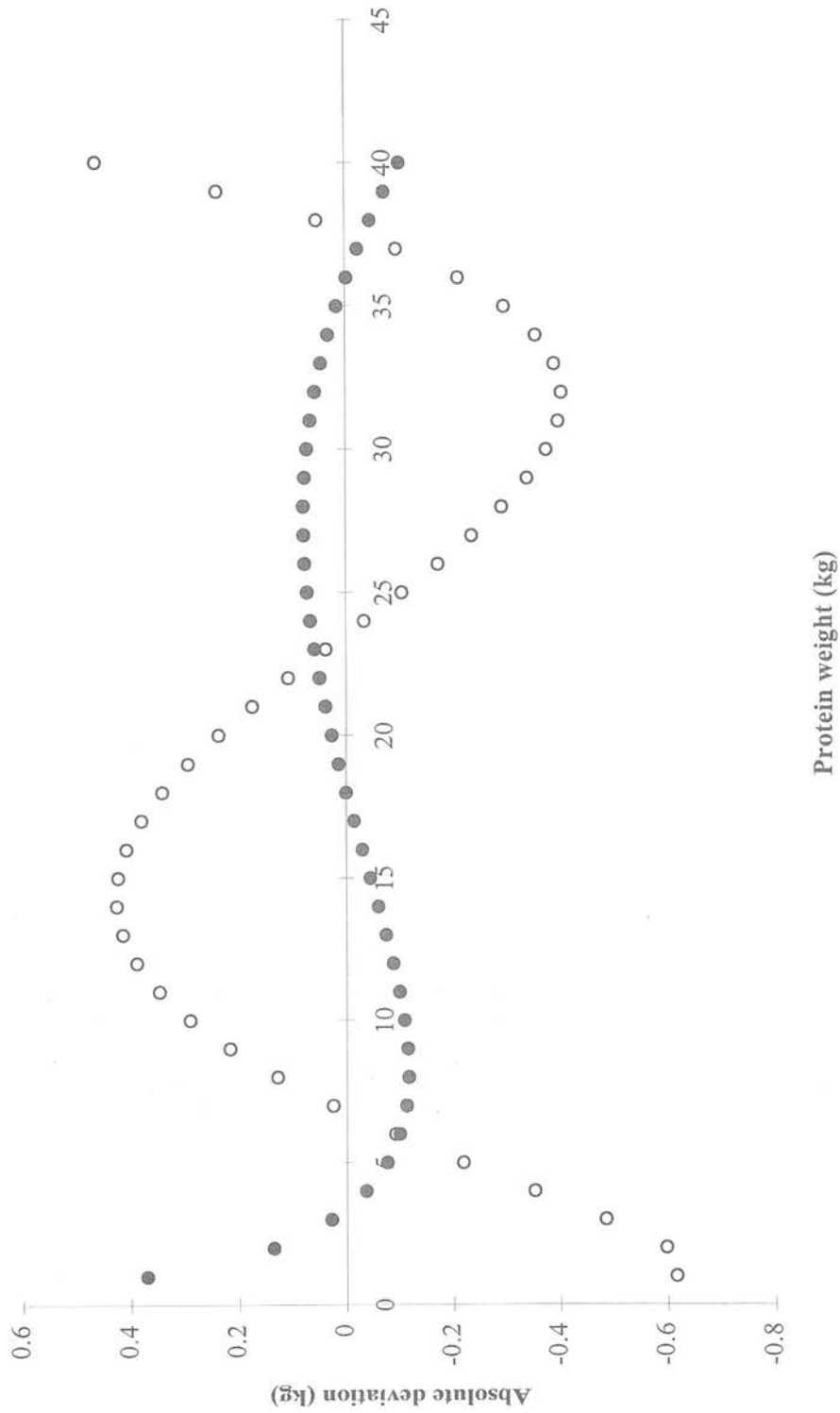
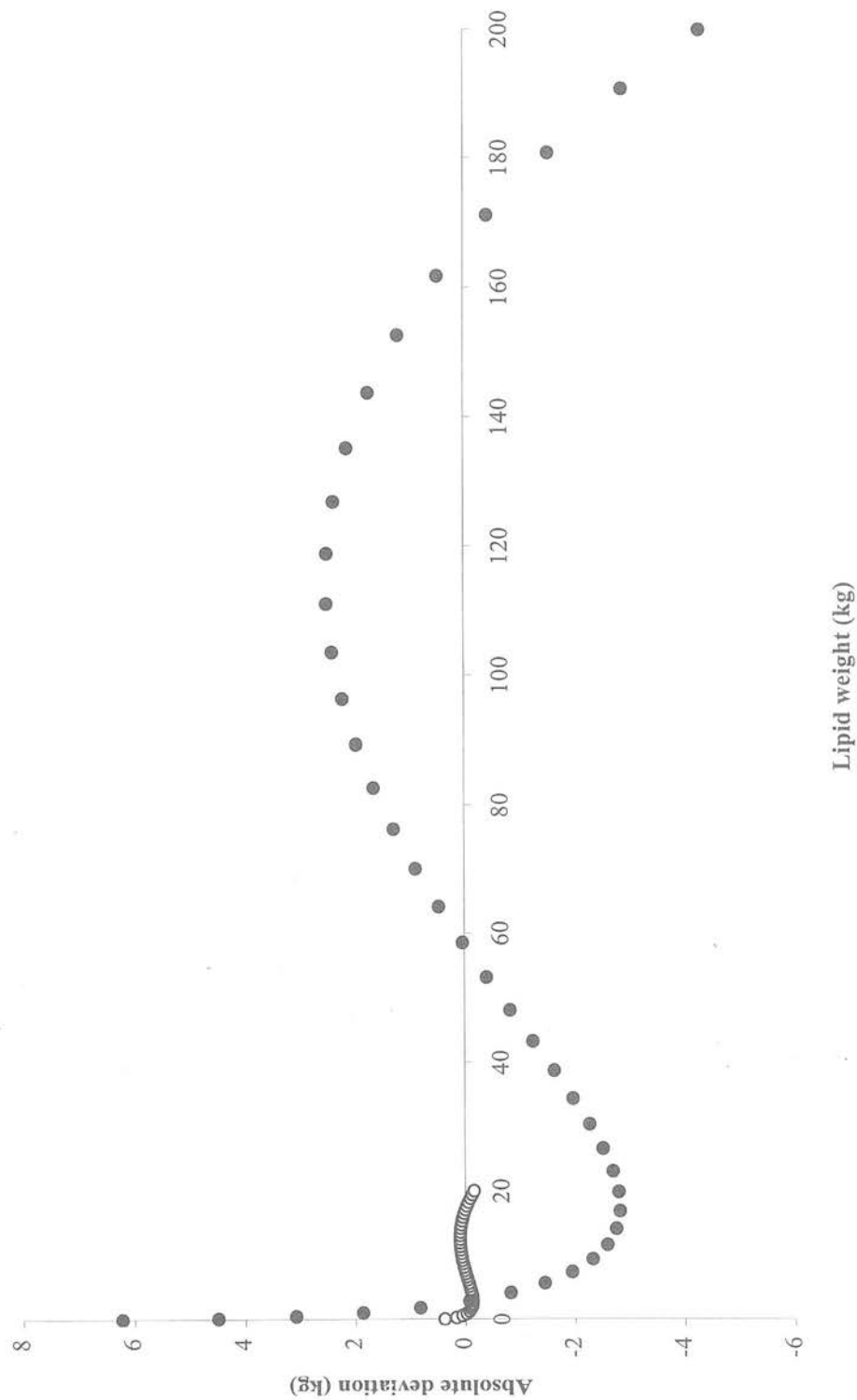


Figure 6.1a. The systematic deviation produced when a quadratic function is used to describe the relationship between protein weight ( $P$ ) and live weight ( $W$ ) at a mature lipid to protein ratio ( $LPR_m$ ) of 0.5 (○) and 5.0 (●).



**Figure 6.1b.** The systematic deviation produced when a quadratic function is used to describe the relationship between lipid weight ( $L$ ) and weight ( $W$ ) at a mature lipid to protein ratio ( $LPR_m$ ) of 0.5 (○) and 5.0 (●).

The value of  $e_g$  can now be estimated as:

$$e_g = y_1 \cdot dP/dW + y_2 \cdot dL/dW \text{ MJ kg}^{-1} \quad (16)$$

The constants  $y_1$  and  $y_2$  are the amounts of energy, MJ, required for the deposition of 1kg of protein and lipid respectively (see Table 6.1a). The total energy required for gain,  $EE_{\text{rqgain}}$  MJ day<sup>-1</sup>, is calculated as:

$$EE_{\text{rqgain}} = (dW/dt)_{\text{max}} \cdot e_g \text{ MJ day}^{-1} \quad (17)$$

It is assumed that the composition of the gain for a particular kind of pig is always the same at a given live weight on a balanced food, irrespective of intake.

### 6.3.2.6 ESTIMATION OF THE BODY COMPOSITION PARAMETERS

The parameters,  $b$  and  $k_1$  in equation 9, for determining the ash content of the gain in the body composition sub model, are taken from Emmans and Kyriazakis (1997). With the value of  $b = 1$  the parameter  $k_1$ , is the ash to protein ratio at all values of  $P$ ; it is assumed to be 0.20. The value of the water exponent  $c$  (equation 10) is also assumed to be constant across genotypes and food (Emmans and Kyriazakis, 1995b) and to have the value of 0.855 (Kotarbinska, 1969). The value of the water scalar  $k_2$  in equation 10 is calculated on the assumption that the ratio of water to protein at maturity ( $WAPR_m$ ) is the same for all pigs and is not correlated with mature protein weight (Emmans and Kyriazakis, 1995b). The value of  $k_2$  is then estimated from

$$k_2 = WAPR_m \cdot P_m^{1-c} \quad (18)$$

where  $WAPR_m$  is 3.04 (Emmans and Kyriazakis, 1995b) and  $c = 0.855$ . The value of  $k_2$  is actually constant because  $P_m$  is assumed to have a constant value of 40kg.

The value of the lipid exponent  $d$  in equation 11 depends on  $LPR_m$ . Emmans (1997) found that the value of  $d$  could be estimated from:

$$d = 1.46.LPR_m^{0.23} \quad (19)$$

The value of  $k_3$  in equation 11 is calculated as:

$$k_3 = LPR_m.P_m^{1-d} \quad (20)$$

The ‘data’ generated by the body composition sub-model in the spreadsheet were used to estimate the values  $b_1$  and  $c_1$  for protein, and  $b_2$  and  $c_2$  for lipid in the quadratic relationships between P and W and L and W for  $LPR_m$  values of 0.5, 1.0, 1.5 ... 5.0 in turn. The values of each of  $b_1$ ,  $c_1$ ,  $b_2$  and  $c_2$  were then made quadratic functions of  $LPR_m$  so that:

$$b_1 = g_1 + h_1.LPR_m + j_1.LPR_m^2 \quad (21)$$

with analogous equations for the other three parameters. The values of  $g$ ,  $h$  and  $j$  for each of  $b_1$ ,  $c_1$ ,  $b_2$  and  $c_2$  are given in Table 6.1b. These relationships were used to estimate the composition of the gain of a pig with a given value of  $LPR_m$  at a given weight.

**Table 6.1a.** *The equations and parameter values used to predict changes in food intake over time during the period of adaptation to a new food*

Component	Equation	Parameter	Value	Units	Reference
$(dW/dt)_{\max}$	$(dW/dt)_{\max} = B \cdot W \cdot \log_e (A/W)$	A	250	kg	Knap 2000
$(dW/dt)_{\max}$	$(dW/dt)_{\max} = B \cdot W \cdot \log_e (A/W)$	B	0.013	d <sup>-1</sup>	Emmans 1988; Knap 2000
$C_{\text{whc}}$	$C_{\text{whc}} = z \cdot W$	z	0.27	Units kg <sup>-1</sup> day <sup>-1</sup>	Chapters 2 and 3
EE <sub>m</sub>	$EE_m = a \cdot W$	a	0.11	MJ kg <sup>-1</sup> day <sup>-1</sup>	Emmans and Fisher, 1986
ASH	$ASH = k_l \cdot P^b$	b	1		Emmans and Kyriazakis,
ASH	$ASH = k_l \cdot P^b$	$k_l$	0.2		Emmans and Kyriazakis,
WA	$WA = k_2 \cdot P^c$	c	0.855		Kotarbinska, 1969
WA	$k_2 = WAPR_m \cdot P^{1-c}$	WAPRm	3.04		Emmans and Kyriazakis,
L	$d = 1.46LPR_m^{0.23}$	d	variable		Emmans, 1997
L	$k_3 = LPR_m \cdot P^{1-d}$	$k_3$	variable	kg kg <sup>-1</sup>	Emmans, 1997
EE	$EE = y_1 \cdot P/W + y_2 \cdot L/W$	$y_1$	50	MJ kg <sup>-1</sup>	Emmans, 1994
		$y_2$	56	MJ kg <sup>-1</sup>	Emmans, 1994

Table 6.1b. The equations and parameter values used to predict changes in body protein and lipid weights with a change in weight

Component	Equation	Parameter	Value
dP/dW	$dP/dW = b_1 + 2c_1W$	$b_1, c_1$	NA
dL/dW	$dL/dW = b_2 + 2c_2W$	$b_2, c_2$	NA
dP/dW	$b_1 = g_1 + h_1.LPR_m + j_1.LPR_m^2$	$g_1$	0.196149
		$h_1$	-0.004645
		$j_1$	-0.0005750
dP/dW	$c_1 = g_2 + h_2.LPR_m + j_2.LPR_m^2$	$g_2$	0.000168
		$h_2$	-0.00017
		$j_2$	0.000022
dL/dW	$b_2 = g_3 + h_3.LPR_m + j_3.LPR_m^2$	$g_3$	0.045183
		$h_3$	0.050894
		$j_3$	-0.00034
dL/dW	$c_2 = g_4 + h_4.LPR_m + j_4.LPR_m^2$	$g_4$	0.0000504
		$h_4$	0.000468
		$j_4$	-0.0000670



### 6.3.2.7 ESTIMATION OF THE ENERGY AND INTAKE PARAMETERS

The value of the parameter  $z$ , used to determine the maximum capacity for WHC in equation 6, was calculated from the data in Chapters 2 and 3. Food intake per kg live weight day, SFI (scaled food intake), was regressed on the reciprocal of the WHC values for a range of bulky foods. The value of  $z$  was estimated to be 0.27 (Table 6.1a). This value is higher than that suggested by Kyriazakis and Emmans (1995) but comparable to the value suggested by Tsaras *et al.* (1998) and may reflect differences in the methodology used to estimate WHC. The value of  $a$  in equation 3 used to calculate the amount of energy required for maintenance, is estimated to be 0.11. It was calculated using the rule of Emmans and Fisher (1986) for scaling maintenance assuming a constant body protein content of 17%. The model is not sensitive to the assumptions made about the energy requirements for maintenance. The values of the parameters  $y_1$  and  $y_2$ , used in equation 16 to determine the amount of energy required per unit of gain, were assumed to be 50 and 56 MJ kg<sup>-1</sup> respectively (Emmans 1994).

### 6.3.2.8 DYNAMIC MODEL

The static model (equations 1 - 21) allows the weight at the end of the day ( $W_1$ ) to be calculated as

$$W_1 = W_0 + \Delta W \quad (22)$$

where with the time step of a day  $\Delta W$  stands for  $dW/dt$  and  $W_0$  is the initial weight. To make the model dynamic, so that equilibrium food intake and growth rate can be predicted over time, the initial weight of the current day is made to equal the final weight of the preceding day. The static model can then be run again so that intake and growth rate on the current day is estimated, the final weight of that day then

becomes the initial weight of the next day and so forth. In this way the model continues to update on a daily basis. It is recognised that updating the model on a daily basis will introduce some degree of error into the model (Emmans, unpublished). However the size of this error will be small and for the purposes of the model the time step of a day is adequate.

### **6.3.3 MODELLING THE TRANSITION FROM ONE FOOD TO ANOTHER**

#### ***6.3.3.1 GENERAL***

The overall aim of the model is to describe the transition to a new equilibrium intake when a change in food type, from one food to another with a different bulk content, occurs. The dynamic model described above predicts the food intake and growth rate for a given pig over time, assuming that food intake is always at equilibrium, i.e., that the pig is fully adapted to the food that it is on. However, when a change in food occurs, from one food to another of higher bulk content there will be a period of adaptation during which food intake will gradually increase until the new equilibrium on the new food is reached. The dynamic model described above makes no attempt to predict changes in food intake and growth rate during such a period of adaptation. Two problems need to be solved to make the model transitory. The first is that the level of food intake on the first day following the change (i.e. the extent to which food intake is initially reduced) must be predicted. Secondly, the model must predict the time course of adaptation, that is, how long it will take for a pig to become adapted to the new food and to reach its new equilibrium intake.

An animal is considered to have a current capacity to consume food bulk (WHC) which is dependant upon the WHC of the food fed and the length of time that the animal has been on that food so that

$$C_{whc} = ((FL.WHC)/W) + v.t \text{ kg kg}^{-1} \quad (23)$$

where, FI is food intake, WHC is the water holding capacity of the food being fed, W is weight, t is time (days) and  $v$  is the daily rate of change in capacity after the changeover. It is proposed that the capacity for WHC on the first day following a change in food will be determined by the WHC of the food fed prior to the change. When an animal is changed from its current food to another food of higher bulk content, capacity for WHC is not expected to change immediately. It is therefore assumed that the capacity for WHC on the first day of the new food will be equal to the current capacity for WHC on the last day of the previous food. Thereafter, capacity for WHC will gradually increase over time as the gastrointestinal tract becomes adapted to the new food being fed (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). The rate of change,  $v$ , is assumed to be the same for all pigs regardless of the food being fed and the increase in capacity over time is assumed to be linear. The available literature on this area is scarce, as in most cases the period of adaptation is not considered. However, the experimental evidence that is available (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998) gives no reason to reject the assumptions put forward. Capacity for bulk after the changeover will therefore be increased to a maximum of  $z$  by  $v$  units per day.

### 6.3.3.2 NEW PARAMETER VALUES

Previous work (Tsaras *et al.*, 1998; Chapter 2; Chapter 3) has shown that adaptation when moving from a food with a WHC of approximately 4kg kg<sup>-1</sup> dry food to a constraining food with a WHC of approximately 8kg kg<sup>-1</sup> dry food takes about 12 days. Therefore, we assume that a pig changing from a food with a WHC of 0kg kg<sup>-1</sup> dry food to a constraining food (8kg kg<sup>-1</sup> dry food) will take about 24 days to adapt to the new food. The maximal capacity for bulk was estimated to be 0.27 units/kg day (Chapter 2 and 3). Consequently, the rate parameter  $v$  is initially assumed to have a value of 0.01 units day<sup>-1</sup>, calculated as 0.27/24.

## **6.4 TESTING THE MODEL**

The model was set up to simulate experiments where an average pig with a given  $LPR_m$  is changed from one food to another with a different bulk content. The model calculates food intake and live weight gain throughout the course of the experiment so that changes in food intake and live weight gain with changes in food type can be monitored.

Preliminary testing of the model was achieved by comparing predicted responses from the model with those recorded in the real system. The data used to evaluate the performance of the model were taken from two studies (Kyriazakis and Emmans, 1995 and Chapter 4) that reported the food intake and performance of growing pigs fed a series of two foods differing in bulk content. In both cases the foods contained varying levels of either unmolassed sugar beet pulp or wheatbran. The model was set up to roughly repeat these experiments. The initial weight, final weight and the live weight at which the food was changed, and the percentage of sugar beet pulp and wheatbran in each of the foods, were inputs to the model. The model was set up so that the relevant food composition variables, DE, CP and WHC were calculated from the percentage sugar beet pulp, SBP, and wheatbran, WB, in the food so that

$$DE = 13.2 - (0.03.SBP) - (0.046.WB) \quad MJ \, kg^{-1} \quad (24)$$

$$CP = 235 - (0.0534.SBP) - (0.819.WB) \quad g \, kg^{-1} \quad (25)$$

$$WHC = 3.5 + (0.093.SBP) + (0.013.WB) \quad units \, kg^{-1} \quad (26)$$

The relationships between food composition and the percentages of SBP and WB were estimated by regressing DE, CP and WHC on the percentage of SBP and WB in the food (data taken from Chapters 2 and 3). SBP and WB are the only two raw materials considered here but the model can be adapted for use with any raw material. DE was then converted to metabolisable energy (ME)

$$ME = (0.997DE) - (0.000189CP) \quad kJ \, kg^{-1} \quad (27)$$

EE was then calculated (Emmans, 1994) as

$$EE = 1.17ME - 4.49CP - 2.44 \quad \text{kJ kg}^{-1} \quad (28)$$

Where ME is in  $\text{kJ kg}^{-1}$ , and CP is the crude protein content ( $\text{g g}^{-1}$ ).

Figure 6.2 shows the individual intakes of a group of pigs during the change over from one food to another of higher bulk content. The variation between pigs is large. This is relevant when comparing the agreement between the predictions of the model and the mean of the observed data.

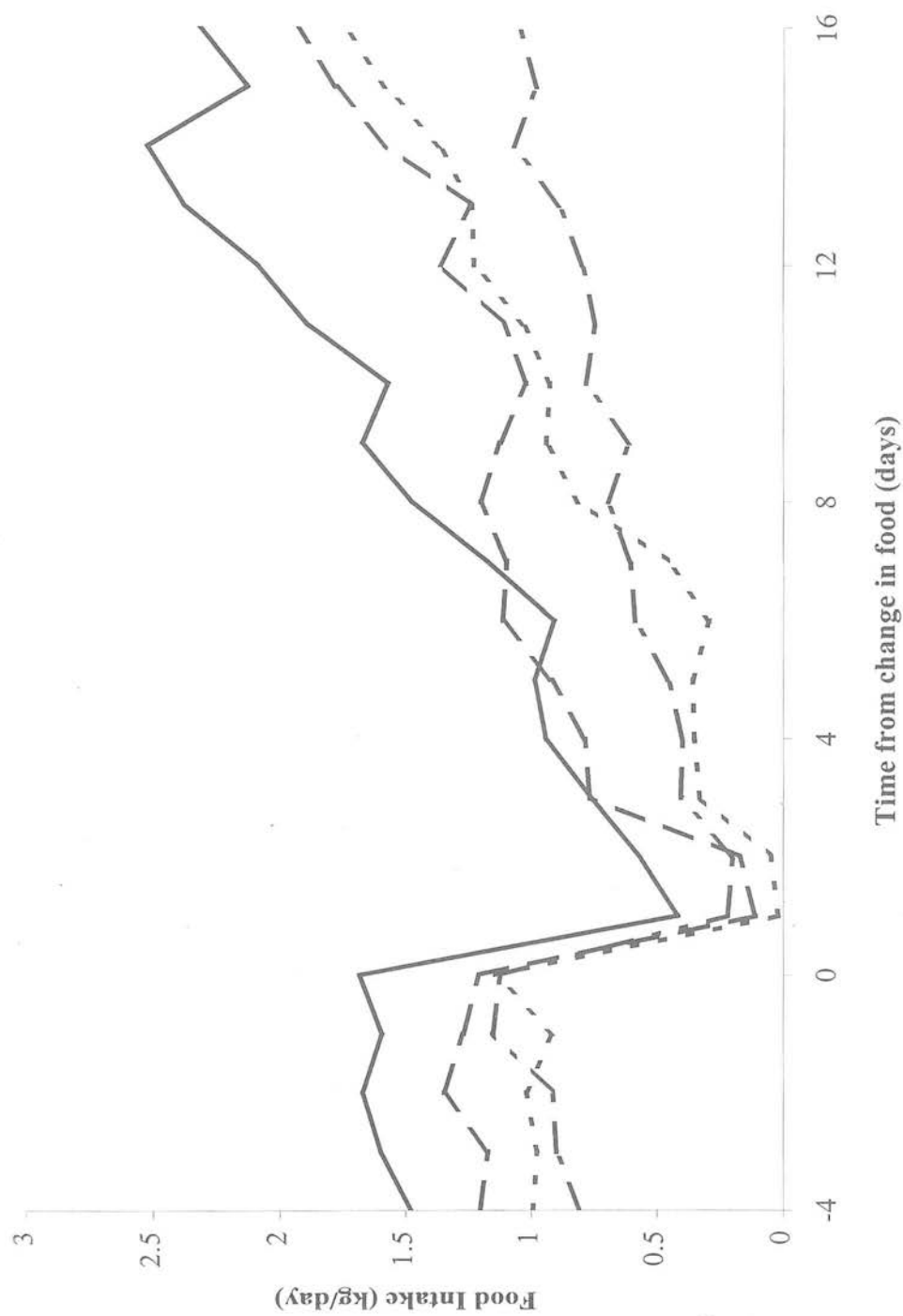


Figure 6.2. Observed food intakes of four pigs changed from a control food to a 97% wheatbran food: data from Kyriazakis and Emmans, 1995

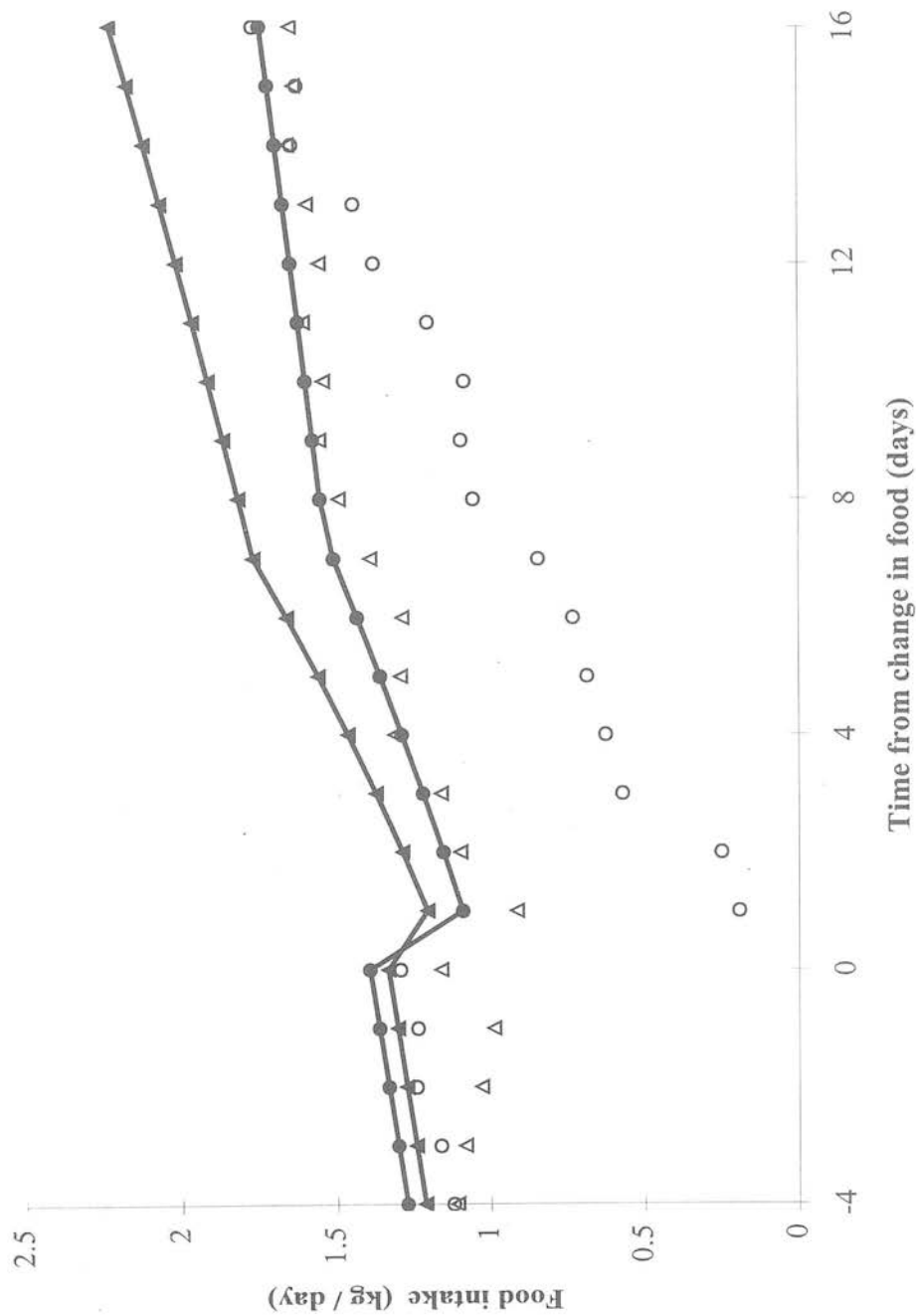
## **6.5 RESULTS**

### **6.5.1 MOVING FROM A CONTROL FOOD TO A BULKY FOOD**

Figure 6.3 shows the predicted and observed food intakes on a change from a control (non-limiting, non-bulky) food to one of higher bulk content. Qualitatively the predictions of the model are in agreement with the measured data of both Kyriazakis and Emmans (1995) and Chapter 4. The model predicts that as the difference in bulk content between the first and second food increases so does the initial reduction in food intake after the change. However, the model consistently under predicts extent of the initial reduction in food intake and hence over predicts food intake on the bulky food when there is a change to a food high in wheatbran.

### **6.5.2 MOVING FROM A LESS TO A MORE BULKY FOOD**

The predictions of the model are in good qualitative agreement with the measured data when the change is from a less to a more bulky food (Figure 6.4). The predictions of the model are in better quantitative agreement with the data of Kyriazakis and Emmans (1995, Figure 6.4a), when there is a change from a 48% wheatbran to a 97% wheatbran food, than those of Chapter 4 (Figure 6.4b), when there is a change from a 70% wheatbran to a 70% sugar beet pulp food. However, for the data of Kyriazakis and Emmans (1995) the model under predicts the extent of the initial reduction in intake after the change. A consequence is that the model over predicts intake after the change. For the data from Chapter 4 the model accurately predicts the initial reduction in food intake after the change in food, but consistently and significantly under predicts food intake on the more bulky food (70% SBP).



**Figure 6.3a.** Observed (open symbols) and predicted (closed symbols) intakes when there is a change from a control food to either a 97% (○, ●) or a 48% (△, ▲) wheatbran food: data from Kyriazakis and Emmans, 1995



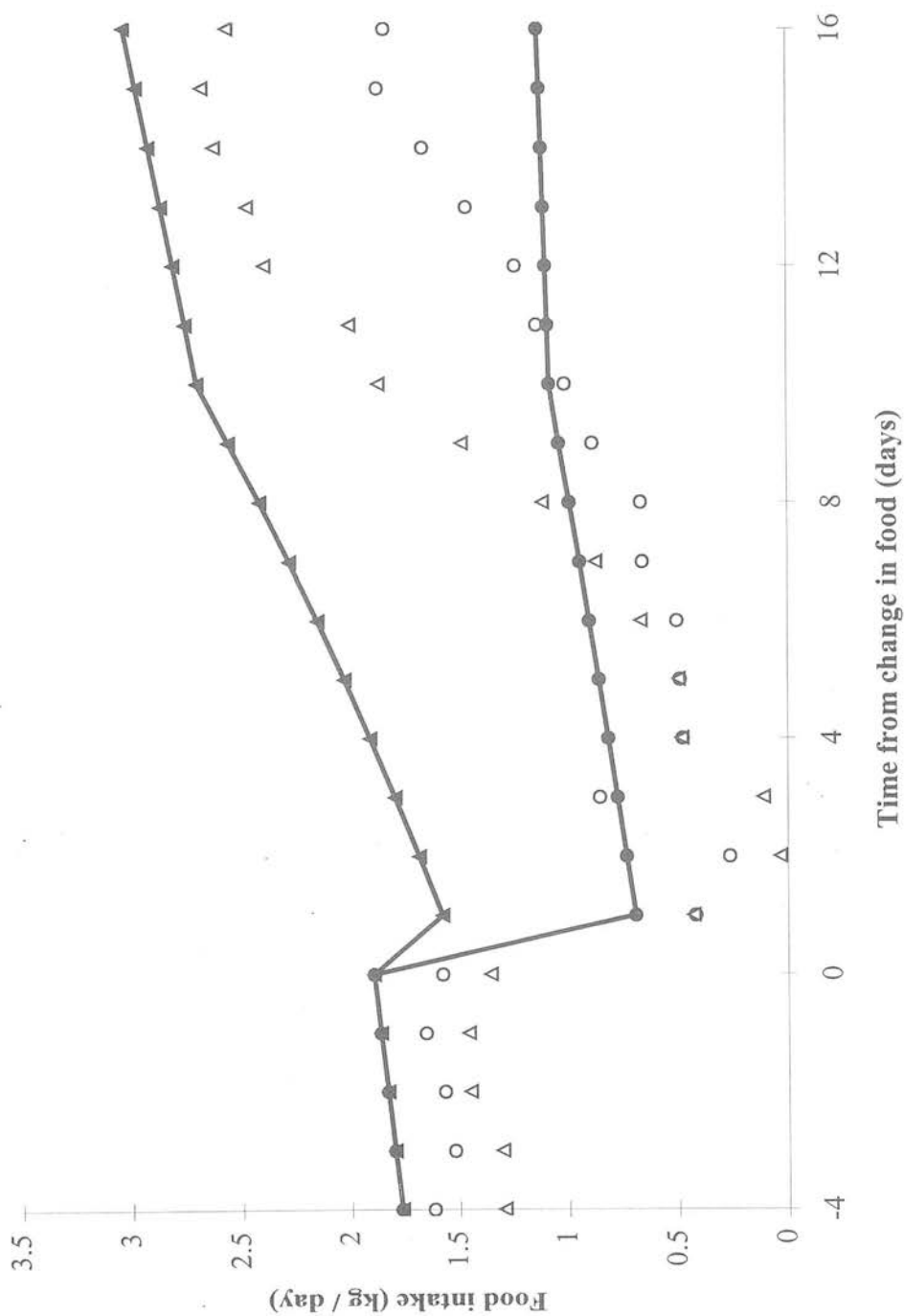


Figure 6.3b. Observed (open symbols) and predicted (closed symbols) intakes when there is a change from a or control food to either a 70% sugar beet pulp food (○, ●) or a 70% wheatbran food (△, ▲); data from Chapter 4.

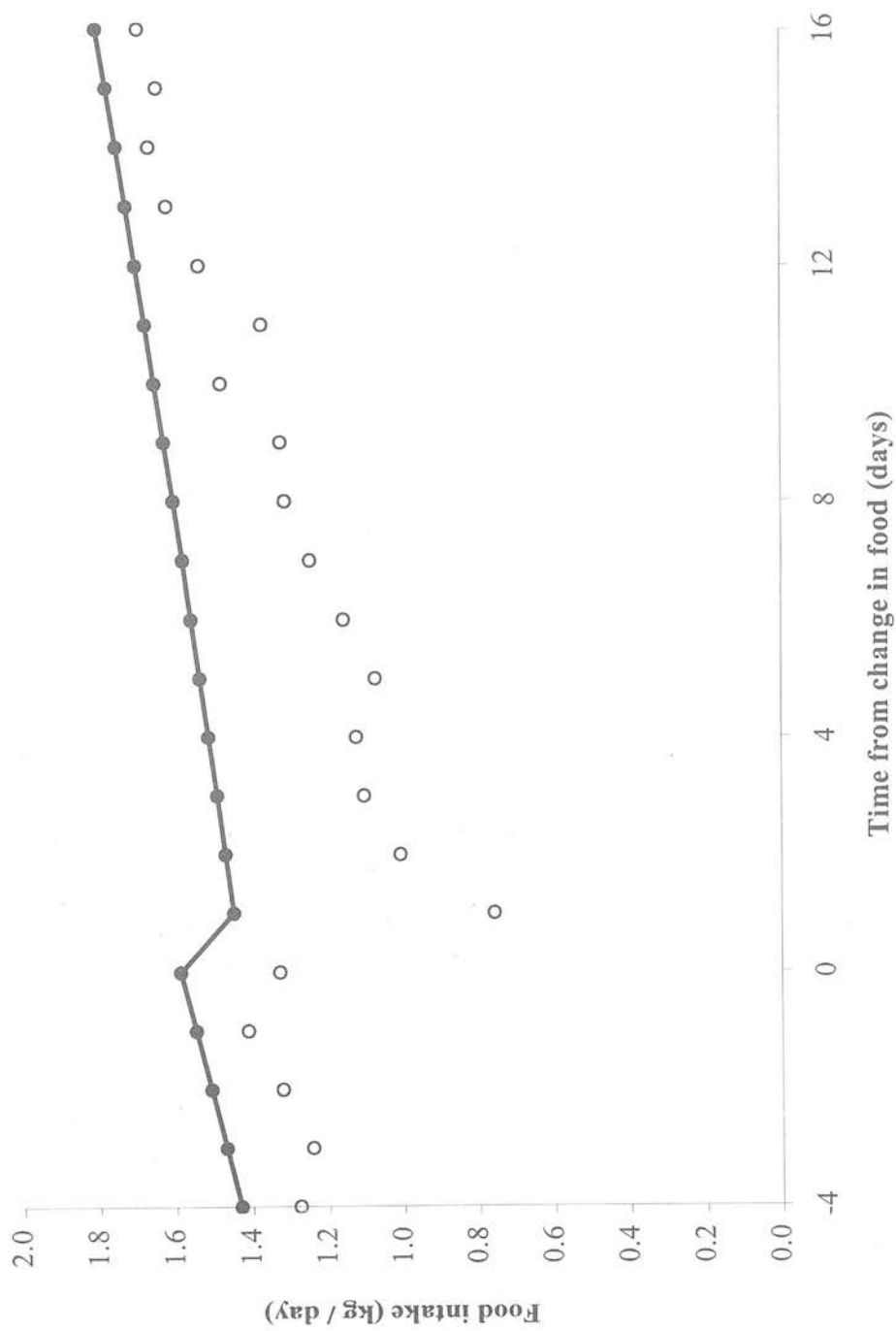


Figure 6.4a. Observed ( $\circ$ ) and predicted intakes ( $\bullet$ ) when there is a change from a 48% wheatbran to a 97% wheatbran food: data from Kyriazakis and Emmans, 1995.

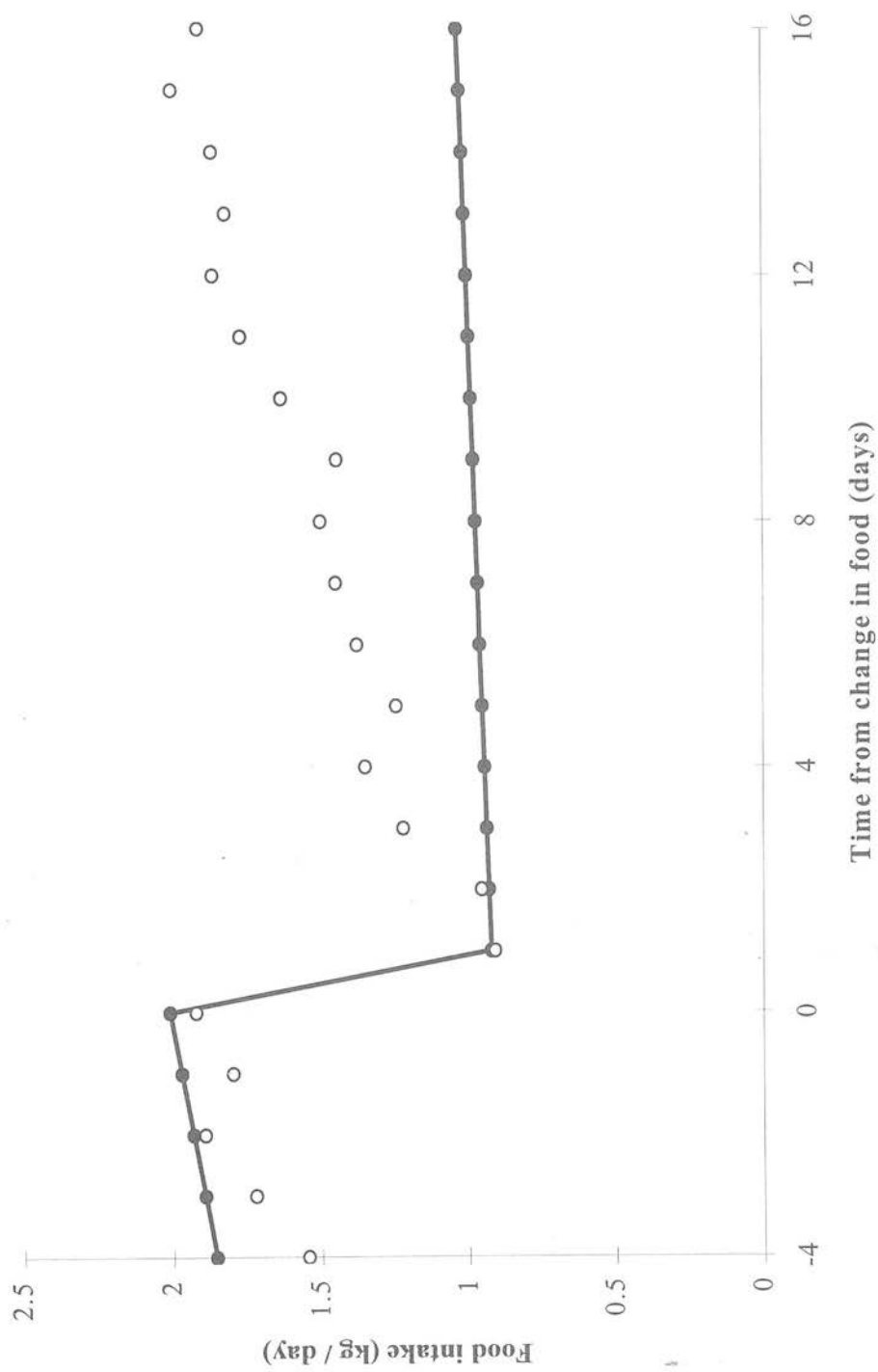
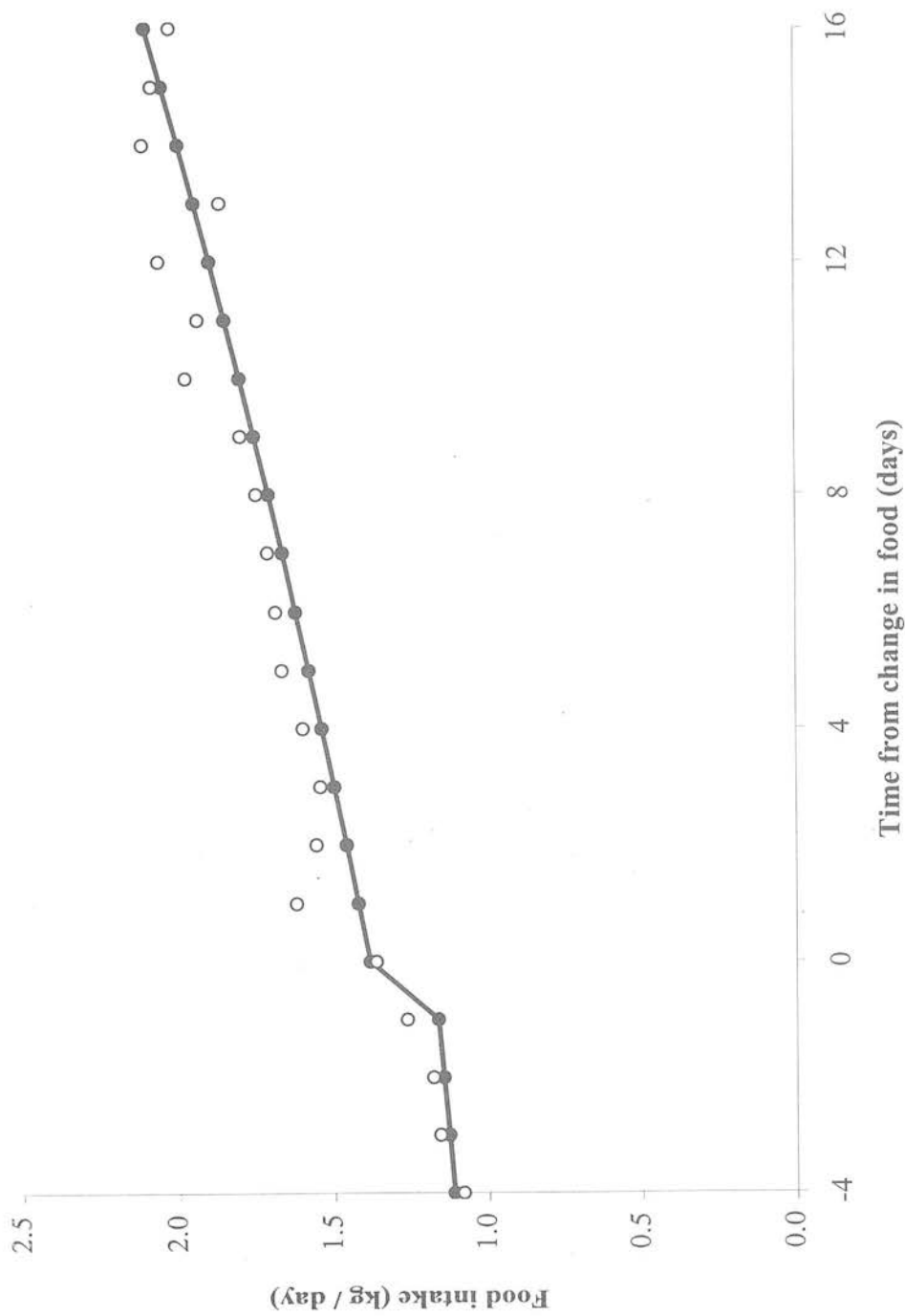


Figure 6.4b. Observed (○) and predicted (●) intakes when there is a change from a 70% wheatbran to a 70% sugar beet pulp food: data from Chapter 4

### **6.5.3 MOVING FROM A MORE TO A LESS BULKY FOOD**

The model predicts the pattern of food intake during such a change with reasonable accuracy (Figure 6.5). The predictions of the model are in good agreement with the data of Kyriazakis and Emmans (1995, Figure 6.5a), where there is a change from a 97% wheatbran food to a 48% wheatbran food. Here the model shows good qualitative and quantitative agreement with the measured data. The model shows good qualitative agreement with the measured data from Chapter 4 (Figure 6.5b), but again under predicts food intake on the less bulky food (70% wheatbran).



**Figure 6.5a.** Observed (○) and predicted (●) intakes when there is a change from a 97% wheatbran to a 48% wheatbran food: data from Kyriazakis and Emmans, 1995.

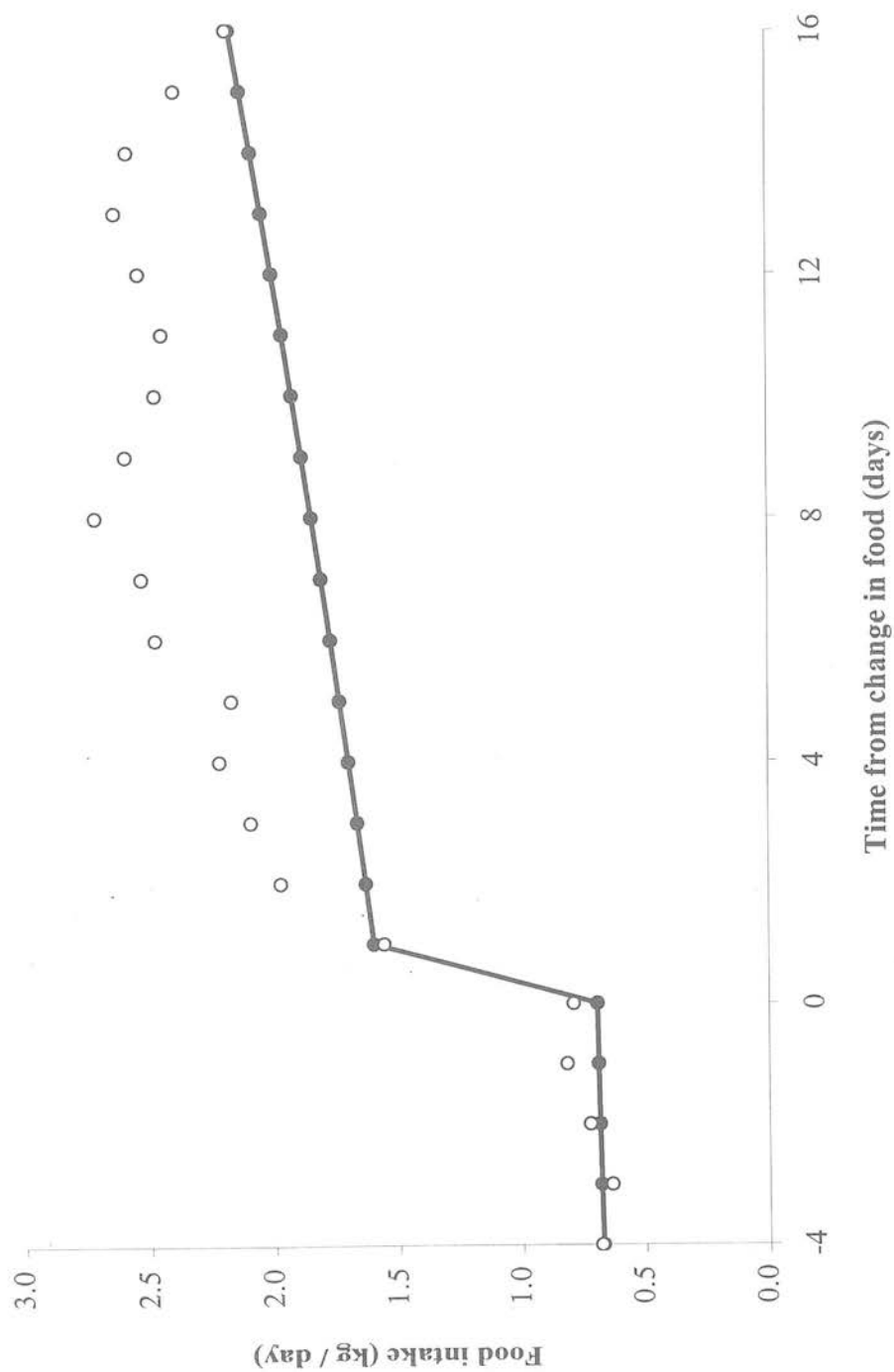


Figure 6.5b. Observed (○) and predicted (●) intakes when there is a change from a 70% sugar beet pulp to a 70% wheatbran food: data from Chapter 4

## **6.6 DISCUSSION**

The aim was to construct a model that could predict intake during the period of adaptation following a change in food type. The assumptions made in the dynamic model, which predicts changes in equilibrium intake over time, were derived from the current literature on dynamic food intake prediction models (Emmans and Fisher, 1986; Emmans, 1988; Emmans, 1994; Emmans and Kyriazakis, 1995b; Kyriazakis and Emmans, 1995; Emmans, 1997; Emmans and Kyriazakis, 1997; Tsaras *et al.*, 1998; Kyriazakis and Emmans, 1999). The model was then adapted to be able to deal not only with intakes when the pig was at equilibrium with its food, but also during the adaptation period to a new food. Most current models to predict food intake do not consider adaptation to a change in food. The adapted model is an initial attempt at describing and quantifying this phenomenon.

### **6.6.1 ASSUMPTIONS MADE IN THE MODEL**

For the purposes of the model it is assumed that the composition of the gain of a given kind of pig at a given weight is unaffected by the type of food being fed. It is recognised that this assumption may not always be correct. It is possible, for example, that on unbalanced foods there will be some differences in composition of gain between foods (Kyriazakis *et al.*, 1991; Kyriazakis and Emmans, 1992a, b). Given that the model is intended to be used only for balanced foods it is likely that any differences in composition of gain between foods will be small enough to be ignored for the present purposes.

The value of the constant  $z$  in equation (6) is crucial for calculating a constrained food intake (CFI). In the current model the value of  $z$  was estimated from the work in Chapters 2 and 3 to be 0.27 units  $\text{kg}^{-1} \text{day}^{-1}$ . This is substantially higher than the value of 0.17 estimated by Kyriazakis and Emmans (1995), but closer to the value of 0.23 estimated by Tsaras *et al.* (1998). The variation in estimates of the value of  $z$

between these cases may be due to differences in the methodology used to measure WHC.

The parameter  $\nu$  is the rate at which the pig's capacity for WHC increases during adaptation. The value of  $\nu$  was estimated to be 0.01 units day<sup>-1</sup>. It is assumed that the rate of change is the same for all pigs regardless of the food being fed and that the increase in capacity over time is linear. It is recognised that the value of constant  $\nu$  and the assumptions made about it may not be correct. However, as a first step the value chosen for  $\nu$  and the assumptions made about it seem reasonable, based on evidence in the literature.

### 6.6.2 MOVING FROM A CONTROL TO A MORE BULKY FOOD

Qualitatively the predictions of the model agree quite well, but far from perfectly, with the measured data when the change is from a control to a more bulky food (Figure 6.3). The model predicts that there will be an initial reduction in intake. The reduction is also predicted to increase as the difference in the bulk content between the two foods is increased. However, the model significantly under predicts the extent to which intake is reduced on the first day after the change over and hence overestimates intake thereafter, particularly when the change is to a food based on wheatbran (see Figure 6.3). In the model the only measure of bulk is WHC and this was found to be sufficient to account for differences in equilibrium intakes (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). The differences in WHC between the control food and the wheatbran foods of Kyriazakis and Emmans (1995) and Chapter 4 are not large. The control food had 3.50g water g dry food<sup>-1</sup> while the 48% wheatbran had 4.12 g water/g dry food, the 70% wheatbran had 4.41g water g dry food<sup>-1</sup> and the 97% wheatbran had 4.76 g water g dry food<sup>-1</sup>. When there is only a small difference in WHC between the foods the model predicts a relatively small reduction in food intake after the changeover. The measured data, where the actual reduction in food intake is much greater than that predicted by the model, suggests



that there may be other factors not considered in the model that are important for the control of intake on food with high contents of wheatbran. Wheatbran has a low digestibility (Ehle *et al.*, 1982; Nyman and Nils-Georg, 1982; Noblet and Bach Knudsen, 1997) with a high level of insoluble, lignified fibre (Ehle *et al.*, 1982; Selvandran, 1984; Noblet and Bach Knudsen, 1997). This fibre is resistant to degradation in the gastrointestinal tract and is only slowly available for fermentation (Noblet and Bach Knudsen, 1997). The large reduction in intake seen following a change to a food with a high wheatbran content may thus be due to the fact that the guts of the pigs are not initially adapted for the digestion of this material. It is unlikely that the microbial population necessary for the efficient digestion of wheatbran will exist immediately following the change. It has been shown that pigs fed high fibre diets have an increased number of cellulose degrading bacteria, and that the cellulolytic activity increases over time (Varel, 1987). The change needed in the microflora population for the efficient degradation of wheatbran can be acquired only over time, as the animal becomes adapted to the food. The model does not account for the fact that different foods may require different amounts of time to reach an equilibrium rate of digestion. In fact, the model does not account for digestion at all, except by using DE values from food Tables, which are presumably equilibrium values. Where the ability to digest wheatbran is important for the control of intake then the model will necessarily under predict the initial reduction in intake after a change to a food with a high content of wheatbran. The problem does not exist when the change is from a control food to one based on sugar beet pulp (Figure 6.3b). The immediate problems of digesting a food based on sugar beet pulp are unlikely to be the same as those for a food based on wheatbran. Sugar beet pulp is a highly digestible material (Nyman and Nils-Georg, 1982). Its high level of pectic polysaccharides enhances microbial attachment allowing a high level of microbial activity, while the high WHC causes swelling which increases the surface area available to the microflora of the gut. All these factors facilitate colonisation and degradation of the substrate (Noblet and Bach Knudsen, 1997). If WHC, rather than the ability to digest sugar beet pulp, determines intake then the model should be able

to accurately predict the initial reduction after a change to a sugar beet pulp food. The evidence (Figure 6.3b) is that it does.

Animals are sometimes said to avoid a food that is new to them, i.e. to show 'neophobia' (Provenza and Balph, 1987; Forbes, 2001). It could be suggested that pigs initially avoided the foods with a high content of wheatbran because it was new to them and they were neophobic. However, if the pigs were neophobic in this case, then they must be expected to be neophobic in general. But they did not show a reduced intake when transferred to the control food after long periods on the foods of high fibre content (Kyriazakis and Emmans, 1995; Chapter 4). They therefore cannot be seen as being neophobic in general, and neophobia cannot account for the initial reduction in intake when there a change to a new food high in wheatbran.

### **6.6.3 MOVING FROM A LESS TO A MORE BULKY FOOD**

The predictions from the model for such a change (Figure 6.4) are also in qualitative agreement with the measured data. As before, however, the model under predicts the reduction in intake for foods based on wheatbran, and a consequence of this is that it over predicts food intake during the initial few days after the changeover. A likely reason for this discrepancy between the model predictions and the observed data has been discussed above. The model is able to predict with a high degree of accuracy the initial reduction in food intake when there is a change from a 70% wheatbran food to a 70% sugar beet pulp food (Figure 6.4b). Thereafter, however, the model significantly under predicts food intake on the sugar beet pulp based food. The reason for this discrepancy is not clear, but it is also seen to occur when there is a change from a control food to a 70% sugar beet pulp food (Figure 6.3b). It is assumed in the model that there is a maximum capacity for bulk ( $0.27 \text{ units kg}^{-1} \text{ day}^{-1}$ ) which cannot be exceeded and that actual capacity will be increased by  $0.01 \text{ units day}^{-1}$  until the maximum is reached. For this particular case, when there is a change in food from a 70% wheatbran food to a 70% sugar beet pulp food, the model

predicts that the maximum capacity for bulk will have been reached by the time that the change in food occurs. In the experiment in Chapter 4 pigs were fed the wheatbran food for a period of 21 days prior to the change over. The increase in intake over time on the sugar beet pulp food is therefore, the result of an increase in liveweight. The observed data show that in reality pigs are able to consume significantly more of the sugar beet pulp food than would have been expected according to the results from other work completed in this area (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998; Chapter 2). It may be that their ultimate capacity for bulk, at least as sugar beet pulp, is much greater than is assumed in the model. If it is assumed that there is no maximum capacity, and that capacity for bulk increases indefinitely at a rate of 0.01 bulk units per day, then the model predictions are in much better agreement with the observed data (Figure 6.6) for a change from a food with 70% wheatbran to one with 70% sugar beet pulp. Here the model is able to accurately predict food intake on a 70% sugar beet pulp food. Despite the good fit of the model to the observed data when there is a change from a 70% wheatbran to a 70% sugar beet pulp food, the assumption that there is no maximum capacity for bulk does not account for the data when there is a change from a 48% wheatbran food to a 97% wheatbran food (Kyriazakis and Emmans, 1995, Figure 6.7). Therefore, this assumption cannot be considered to be general. The validity of the assumption that there is no maximum capacity for bulk must also be questioned. It does not seem sensible to assume that the capacity for bulk will increase *ad infinitum*.

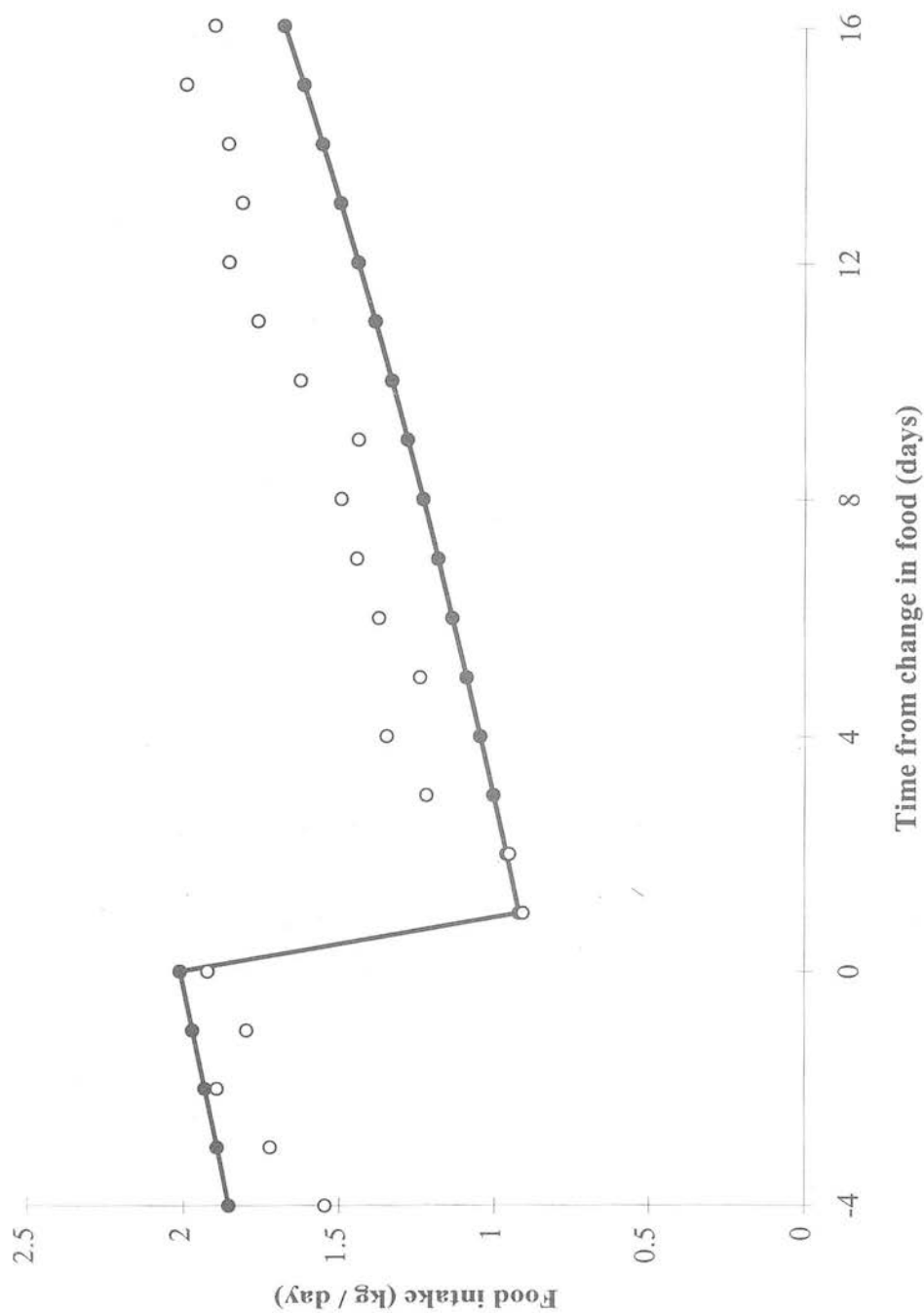
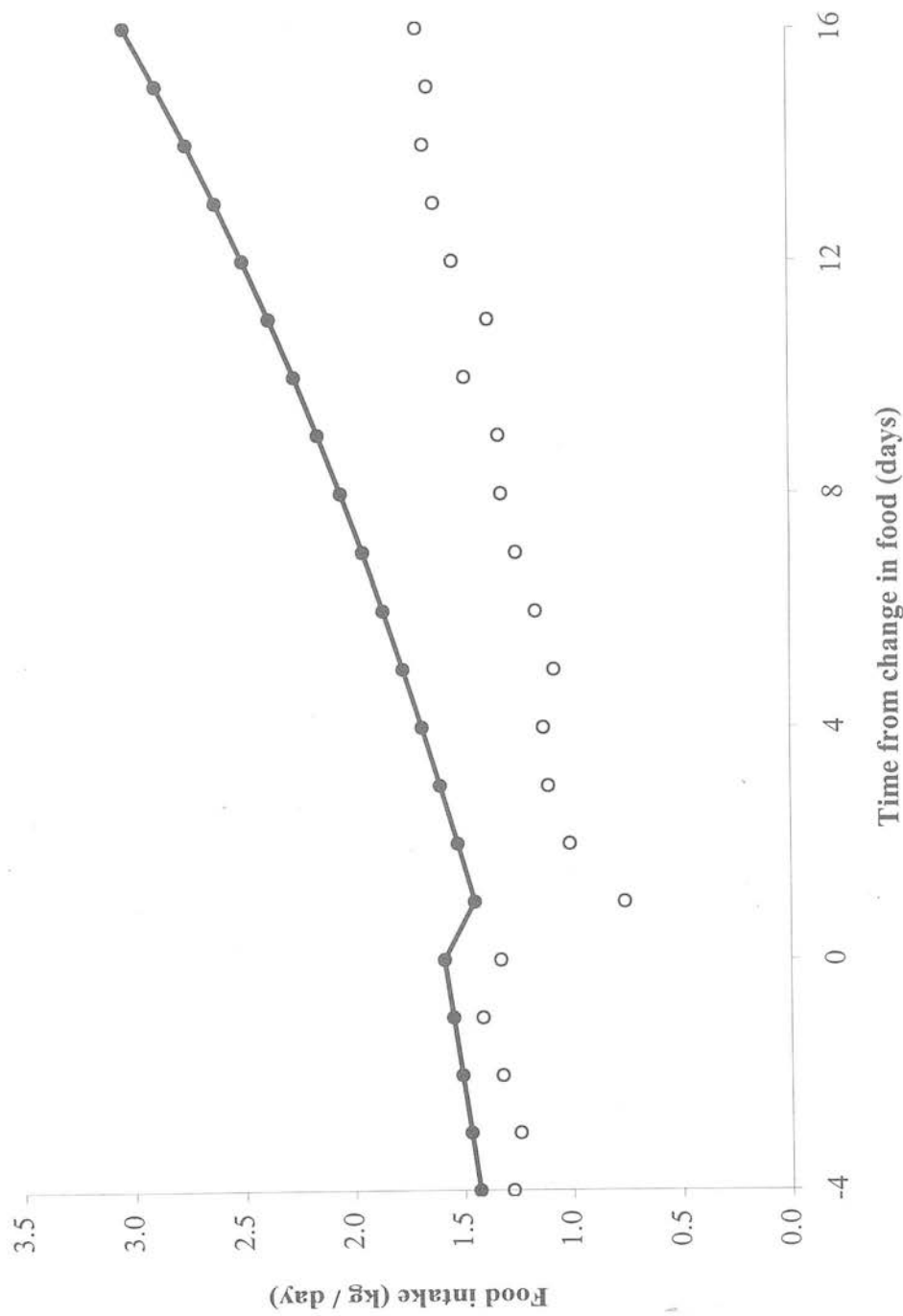


Figure 6.6. Observed ( $\circ$ ) and predicted ( $\bullet$ ) intakes when there is a change from a 70% wheatbran to a 70% sugar beet pulp food. The predicted data are those produced by the model when it is assumed that there is no maximum capacity for bulk: data from Chapter 4.



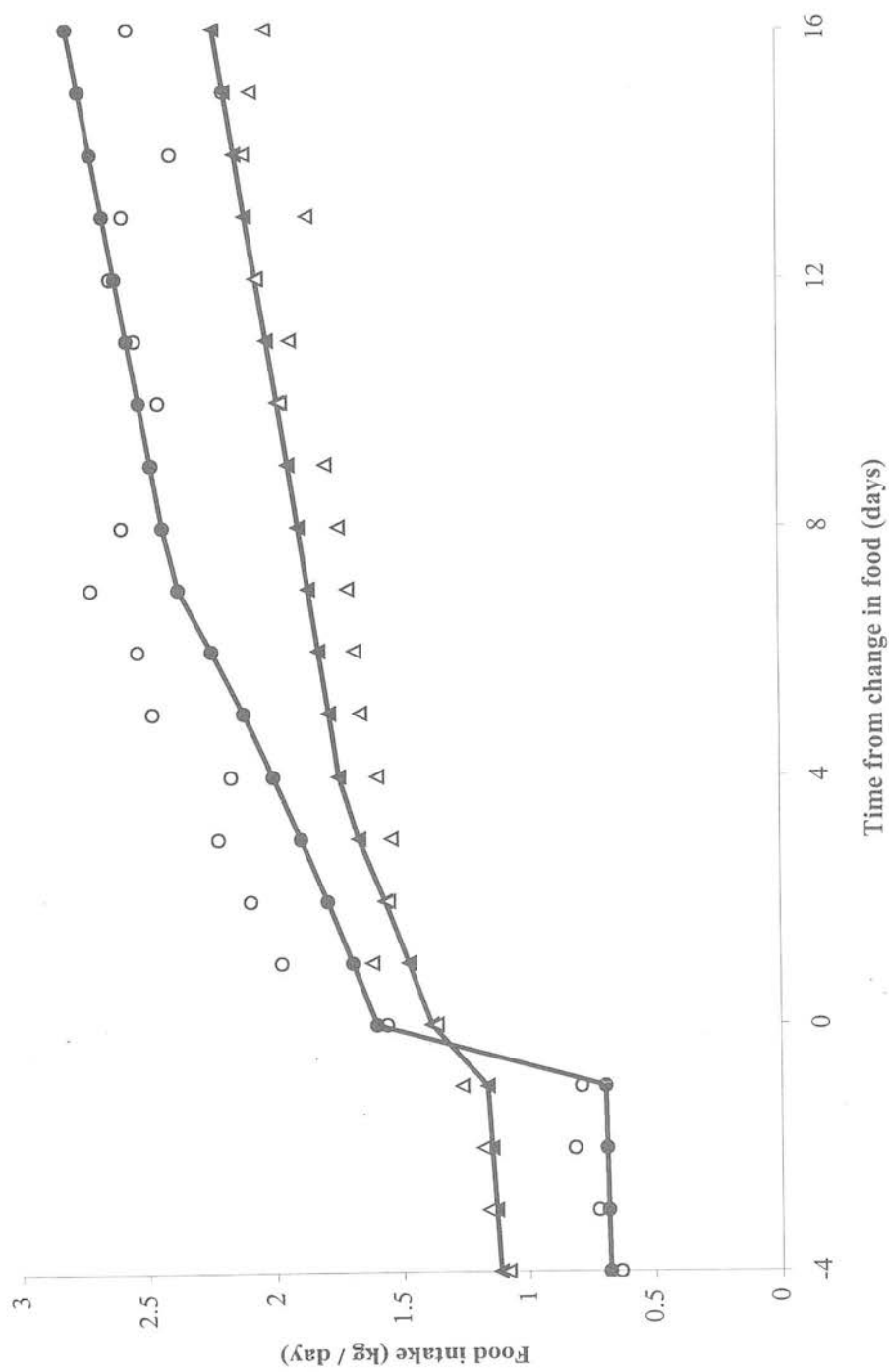
**Figure 6.7.** Observed (○) and predicted (●) intakes when there is a change from a 48% wheatbran to a 97% wheatbran food. The predicted data are those produced by the model when it is assumed that there is no maximum capacity for bulk: data from Kyriazakis and Emmans, 1995.

#### 6.6.4 MOVING FROM A MORE TO A LESS BULKY FOOD

The model provides a very accurate fit to the observed data of Kyriazakis and Emmans (1995) when the change is from a food with 97% wheatbran to one with 48% wheatbran (Figure 6.5a). However, the model under predicts the intake of a 70% wheatbran food when the change is from one with 70% sugar beet pulp food using the data of Chapter 4 (Figure 6.5b). This discrepancy can probably be attributed to the fact that the model makes no attempt to account for any compensatory increases in food that may occur when moving from a bulky food to one of improved quality. It has been shown that when animals are released onto a food of improved quality after a period of feeding on a high bulk food subsequent compensatory intakes and gains occur (Robinson, 1964; Owen *et al.*, 1971; Stamataris *et al.*, 1985; Chapter 3). The data from Chapter 4 shows that the 70% wheatbran food was not a constraining food when fed under the circumstances depicted in Figure 6.5b. It therefore seems likely that when pigs were moved from the sugar beet pulp food onto the wheatbran food that some compensatory increase in intake and gains would occur and certainly the food intake data seem to suggest that this is the case. Under conditions where compensation occurs the model would be expected to under predict intake on the second food because it does not account for the occurrence of compensatory increases in intake. For the same reason the model would not be expected to be able to accurately predict changes in food intake over time when a change from a bulky food to a control food occurs. Here, also, compensatory increases in intake would be expected to occur (Chapter 3). To predict changes in intake when there are increases in intake to support compensatory gains are out with the scope of this model.

Figure 6.8 shows the model predictions when a change from a bulky food to a less bulky food is considered and the assumption that there is no maximum capacity for bulk is made. Here, the model predictions show good agreement with the observed data. The reason for the agreement could be that in the cases of both Kyriazakis and Emmans (1995) and from Chapter 4 the food fed after the change over was not

constraining food intake. The data from Chapter 4 and Kyriazakis and Emmans (1995) show that neither the 70% wheatbran nor the 48% wheatbran food was limiting at the time they were fed and that growth rates on both were comparable to that achieved on the control food. If the food is not constraining then animals will be able to meet their desired food intake (DFI) and hence the capacity to consume food bulk and whether or not there is a maximum capacity, are both irrelevant.



**Figure 6.8.** Observed (open symbols) and predicted (closed symbols) intakes when there is a change from a 70% sugar beet pulp food to a 70% wheatbran food (○, ●) or from a 97% wheatbran food to a 48% wheatbran food (△, ▲). The predicted data is that produced assuming that there is no maximum capacity for bulk: data from Kyriazakis and Emmans, 1995 and Chapter 4



## **6.7 CONCLUSIONS**

The model was designed to be able to predict changes in food intake over time during the period over which adaptation to the new food occurs. Qualitatively the predictions of the model are in close agreement with relevant observed data in at least some cases. We conclude that the underlying theoretical assumptions of the model are reasonable. The main failures of the model are (1) prediction of initial intake on being changed to foods of high wheatbran content and, (2) prediction of intake of a non-limiting food where compensatory intake and gain occur. It may be possible to adapt the model to overcome the first reason for failure by dealing explicitly with the time course of digestive efficiency following the change to a new food. To deal with the second reason for failure would need a sufficient understanding of the time course of compensatory growth. This is not currently available.

# **CHAPTER 7**

## **General Discussion**

## **7.1 INTRODUCTION**

Currently there is a lack of understanding about the factors that are important for the control of food intake on high bulk foods. This makes accurate food intake prediction difficult. The objective of this thesis, therefore, was to investigate the factors that are important for the control and prediction of food intake in pigs fed bulky foods.

The aim of chapters 2 - 4 was to use experiments to distinguish between the two frameworks currently available for the understanding and prediction of food intake. The first two experiments (Chapters 2 and 3) were designed to test areas where the frameworks differed in their predictions for high bulk foods. In Chapter 4 hypotheses were developed about the way in which a physical constraint to food intake might operate and how this might affect short term feeding behaviour (STFB).

Chapters 5 and 6 were concerned with improving methods of food intake prediction for high bulk foods. Chapter 5 tested, experimentally, whether predictive methodologies developed for use in young growing pigs could be extended for use in more mature pigs. In Chapter 6 an attempt was made to develop a model that would predict food intake during the adaptation period when there is a change in food to one of higher bulk content. Most food intake prediction models assume that the animal is always fully adapted to the food that it is being offered and do not account for the immediate effects of a change in food type upon food intake. The model in Chapter 6 represents an initial attempt at describing the phenomenon of adaptation.

The purpose of this final chapter is to bring together the findings of the previous chapters and to further discuss them with reference to the current literature. The implications of the findings of this thesis for the understanding and prediction of food intake on high bulk foods will be discussed. Areas where more research is required will be highlighted and suggestions for future research will be made.

## **7.2 A FRAMEWORK FOR THE UNDERSTANDING AND PREDICTION OF FOOD INTAKE IN PIGS**

Currently most models aimed at predicting the food intake of pigs fed high bulk foods assume that animals aim to achieve a desired level of food intake determined by genetic potential, unless, intake is constrained in some way (see section 1.2.1). In recent years, however, this view has been strongly criticised (e.g. Grovum, 1986; Ketelaars and Tolkamp, 1992; Tolkamp, 1999, see section 1.2.2). In response to these criticisms Tolkamp and Ketelaars (1992) developed an alternative framework for the understanding and prediction of food intake. According to this framework, an animal aims to optimise, not maximise, food intake so that maximum efficiency (defined as the rate of net energy intake per unit of oxygen consumed) can be achieved (see section 1.2.3). The framework of (Tolkamp and Ketelaars, 1992) was developed in ruminants but is assumed to be general, although thus far it has only been quantified for mature sheep. It is important to distinguish between these two frameworks if accurate food intake prediction is to be achieved.

The aim of the experiments in Chapters 2 and 3 was to distinguish between the two frameworks described above. The frameworks differ in their predictions of the effect that a reduction in temperature will have upon the intake of a constraining food (Chapter 2) and the effect that a period of reduced growth will have on the subsequent intake of a constraining food (Chapter 3). Experiments were designed that investigated these factors to provide a severe test of the frameworks.

The results of Chapter 2 were clearly in agreement with the idea that animals aim to maximise performance subject to constraints. There was a highly significant interaction between food and temperature. Intake was increased by a reduction in temperature on a low bulk control food but not on a high bulk food. This agrees with the view that high bulk foods physically constrain intake.

In Chapter 3 the effect of a period of reduced growth on the subsequent intake of a high bulk food was investigated. In this experiment after a period of reduced growth

pigs were given access to either a control food or a constraining food which had a 'moderate' bulk content (35% or 56% SBP). Although there were problems with the degree to which the moderately bulky foods were limiting, the results from Chapter 3 were more closely in agreement with the idea that animals aim to maximise performance subject to constraints. The ability to increase intake after a period of restricted growth was significantly less on a bulky food than on the control food, a finding that was not in agreement with the idea of maximum efficiency. Although it was intended that the high bulk foods used in this experiment should be constraining, i.e. limit the intake and the performance of the pigs to which they were fed, it was shown that adapted performance on the moderately bulky foods with 35 or 56% sugar beet pulp was comparable to that achieved on the control food. If the assumption that animals aim to maximise efficiency were correct, it would have been expected that the increase in intake after a period of reduced growth would have been similar on the two foods, which it clearly wasn't.

In Chapter 4 the effect of foods differing in bulk content on STFB was investigated. It was expected that foods differing in bulk content would have different levels of intake, which would be reflected as differences in STFB. Although literature on the effects of food bulk on STFB is scarce, hypotheses about the way in which a physical constraint might affect STFB were developed. H1 was that on bulky foods there would be less diurnal variation in feeding. H2 was that STFB would be less flexible on foods with a high bulk content so that when feeding time was limited, STFB would not be able to be altered in a way that the restriction imposed would be overcome. H3 was that when the food offered was changed STFB would be rapidly altered to suit the new food. In general, the observed differences in STFB were consistent with those expected to occur if a bulk constraint to intake was present. STFB was shown to be less flexible on high bulk foods and, when there was a change in food, STFB was rapidly altered to suit the new food.

It had been hypothesised that on bulky foods there would be less diurnal variation in feeding on high bulk, perhaps even with feeding being extended into the night. However, contrary to expectations, there was no difference in either the diurnal

pattern of feeding or the proportion of feeding that occurred during the night between the foods. The lack of any effect of bulky foods on the diurnal pattern of feeding has been found in other work (e.g. Walker, 1991 for pigs, Johnson *et al.*, 1986, for rats and Tolkamp *et al.*, 2002, for cattle). In the work in cattle (Tolkamp *et al.*, 2002) this result was taken as evidence that physical constraints are not important for the regulation of food intake. It is suggested, however, that in actual fact the opposite may be true. If physical fill builds up gradually throughout the course of a day until a maximum is reached, it is possible that the level of fill will prevent feeding from being extended in to the night. If this assumption is correct then it might be expected that the number of visits made per hour would gradually be decreased as physical fill increased throughout the day. On all foods there was a peak of feeding activity in the morning that coincided with the pigs being fed. However, on the SBP food, in contrast to the other foods, there was a decline in the number of visits made per hour throughout the afternoon. This decline in visit number provides some evidence in favour of the hypothesis that physical fill increases gradually throughout the day.

It might be expected that on high bulk foods feeding would occur at more regular intervals so there would be less variation in the number of visits occurring per hour. However, it was clear from Chapter 3 that this was not the case, even on the most limiting food there was an extensive increase in feeding activity in the morning. More regular intervals between feeding might be expected to occur if the physical constraint to food intake operates at the level of the stomach. If the size of the stomach was physically constraining, on high bulk foods animals would be expected to become physically full at a lower level of intake and hence smaller meals might occur. Because animals would be expected to eat to a constant level of fill these meals might occur at more regular intervals.

Data about the way in which meal patterns were affected by bulk content could not be collected in Chapter 3. It was originally intended that the data would be analysed in terms of both visits and meals. It was hoped that the visit data would be used to determine a meal criterion (the longest non-feeding interval considered to be part of a meal) for each food so that visits could be grouped into meals. However, it was

found that throughout the course of the experiment the FIRE system, as adapted here for individual pigs, was not successful in accurately recording the amount of food eaten in a visit. Without an accurate record of food intake per visit it was not possible to identify and remove from the data the visits during which no feeding occurred ('exploratory' visits). This led to unrealistic estimates of meal criteria and hence visits were not able to be accurately grouped into meals. Although, information about the way in which visits are distributed throughout the day cannot, strictly, be taken to provide evidence about the way in which meals will be distributed, the data from Chapter 3 showing that visits do not occur at more regular intervals on high bulk foods does provide some evidence that the stomach is not the site of an important physical constraint to food intake.

It was concluded from the results in Chapters 2 - 4 that there is no evidence to reject the idea that animals aim to maximise performance subject to the presence of constraints. Most of the variation in food intake and the changes seen to occur in STFB in response to bulky foods could be explained by the idea that intake is physically constrained.

### **7.2.1 THE BIOLOGICALLY RELEVANT UNIT FOR STFB**

Work done in cattle suggests that the biologically relevant unit of STFB is meals (Tolkamp *et al.*, 2000), not visits as was recorded in Chapter 3. Tolkamp *et al.* (2000) found that the probability of cows ending a visit did not change much with visit length, i.e. that it was a random process. When visits were grouped into meals, however, the probability of cows ending and starting a meal increased with meal length and interval between meals. This result is in agreement with the idea that satiety will decrease as the time since the last meal increases. It was concluded, therefore, that meals were the biologically relevant unit for STFB.

In group-housed animals similar intakes are achieved through widely different combinations of visit size and number (Tolkamp *et al.*, 2000). These differences can

be attributed to innate differences between animals but also to social hierarchy and even to differences in feeder type. Although, all allelomimetism cannot be excluded, the pigs used in the experiment in Chapter 3 were individually housed and the effects of social hierarchy and differences in feeder type were removed as far as possible. Under these conditions visits may be more applicable as a unit for STFB.

Although the point made in the paper of Tolkamp *et al.* (2000) is accepted, the differences in STFB as measured by visits were significant and cannot be ignored. As meals are made up of a cluster of visits, the measurement of meals only may have led to subtle differences in STFB (at the level of visits) being obscured. The use of visits is felt to be, not only justified but also necessary in this case.

Grouping visits into meals would not have changed either the hypotheses or the conclusions drawn from the experiment. In a purely formal sense daily intake must be the product of the number of meals in a day and the average intake in a meal. As changes in intake must reflect, as with visits, a change in meal size, meal number or both, H1, H2 and H3 would not have been different. However, information about the way in which high bulk foods affect meal patterns would have given a more comprehensive view of the way in which high bulk foods affect STFB. Analysis of meals would also, as indicated above, have provided some information about where in the gastrointestinal tract the bulk constraint operated. For example if the stomach were assumed to be the constraining organ, it would be hypothesised that meal size would be reduced but meal number would be increased on high bulk foods. As an example to illustrate the point, a pig given a control food may consume a 1200g of food in a day in 4 meals, intake per meal is thus 300g. If it is assumed that the physical size of the stomach constrains intake then on a constraining food where intake may be 800g per day, the amount able to be consumed in each meal might only be 100g, therefore there would be 8 meals in a day. It is more difficult to make predictions about the way in which meal patterns would change if the constraint operates in the lower section of the gastrointestinal tract (there is a continuous flow of digesta into the lower sections of the GIT, the effects of passage rate and dilution also need to be considered). Although, it is reasonable to assume



that if the constraint does not operate in the stomach then it must operate further down the GIT.

## **7.3 PREDICTING THE FOOD INTAKE OF HIGH BULK FOODS**

The work completed in Chapters 2 – 4 provided no evidence to reject the idea that food intake in young growing pigs is physically constrained on high bulk foods. Chapters 5 and 6 therefore, looked at improving the current methodologies in use for predicting the intake of bulky foods.

### **7.3.1 THE RELATIONSHIP BETWEEN CAPACITY FOR BULK AND LIVWEIGHT**

Kyriazakis and Emmans (1995) and Tsaras *et al.* (1998) showed that for pigs weighing between 12 and 40 kg the maximum capacity to consume food bulk was proportional to liveweight. Although appropriate for the weight range used in these experiments it is not known if this scaling rule will be suitable for use in heavier pigs. This was investigated in Chapter 5.

If the scaling rule adopted by Kyriazakis and Emmans (1995) and Tsaras *et al.* (1998) holds across liveweights, then the SFI (food intake scaled to liveweight  $\text{g kg}^{-1} \text{day}^{-1}$ ) of a bulky food would be expected to be constant across liveweights. However, it was shown in Chapter 5 that SFI and the scaled capacity for bulk were not constant across liveweights, therefore the scaling rule did not hold across the whole relevant weight range. For the weight range of interest of 12 – 120kg, the way in which absolute capacity for bulk (Cap) changed with liveweight (W) was described well by the quadratic function

$$\text{Cap} = (0.230.W) - (0.000476.W^2) \quad \text{units day}^{-1} \quad (\text{rsd } 1.19) \\ (\text{s.e. } 0.03007) \quad (\text{s.e. } 0.0002883)$$

The above function predicts that maximum capacity will be reached at a weight which is not very different to a likely mature weight (Knap, 2000), and predicts, in agreement with the work of Kyriazakis and Emmans (1995), that scaled capacity for bulk is proportional to liveweight between 12 and 36kg. Thereafter, it is clear, however, that this approximate rule does not hold. The above quadratic function predicts that scaled capacity for bulk (units kg<sup>-1</sup> day<sup>-1</sup>) will be 0.224 at 12kg, 0.213 at 36kg, 0.196 at 72kg and 0.179 at 108kg. A decline in the rate of increase in absolute capacity for bulk with an increase in weight is in agreement with the results of work done in growing sheep (Emmans and Friggens, 1995). Here, the entire males of five different breeds of sheep, of different mature weights, were fed a test diet of chopped hay at three different liveweights, the maximum of which was approximately half mature weight. Emmans and Friggens (1995) found that for all five breeds used the rate of increase in absolute intake declined with increasing liveweight.

The quadratic equation predicts that above a weight of 242kg absolute capacity for bulk will begin to decline. Relating absolute capacity for bulk (Cap) to liveweight (W) using the exponential equation

$$\text{Cap} = 42.1 (1 - e^{-0.00564W}) \quad \text{units day}^{-1} \quad (\text{rsd } 1.16)$$

(s.e. 19.3)    (s.e. 0.00338)

where 42.1, is an estimate of the maximum and -0.00564 is a constant, may make more sense biologically as this function does not predict a decline in absolute capacity above 242kg. However, the exponential function is no more accurate than the quadratic over the weight range of interest. As the quadratic function predicts that absolute capacity will only begin to decline above a weight (242kg) that is near maturity, there is no benefit in using the more complicated exponential function.

It is common for capacity for bulk and constrained food intake (CFI) to be calculated as a function of liveweight (e.g. Black *et al.*, 1986; Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998; Whittemore, 1998; Kyriazakis and Emmans, 1999). Indeed, this is the approach that has been adopted throughout this thesis. However, there is some

evidence to suggest that current protein weight might be a better scalar than liveweight for capacity for bulk. Food intake on bulky foods is likely to be closely related to the size of the gastrointestinal tract. At the same protein content, differences in liveweight will be due mainly to differences in fat content. It seems unlikely that differences in lipid weight will affect capacity for bulk (Tsaras *et al.*, 1998). Therefore the use of current protein weight may be more accurate than the use of liveweight. Despite this, capacity for bulk and CFI were related to liveweight and not protein weight in both Chapters 5 and 6. The use of protein weight in the model in Chapter 6 would have required the model to predict whole pig growth, which was not the aim of the model. In addition to this protein content was not expected to change much over the weight range of interest and hence little extra accuracy would have been gained by using protein weight rather than liveweight. Capacity for bulk could not be related to protein weight in Chapter 5 simply because no measurements of protein weight were made.

### **7.3.2 THE GIT AND FOOD INTAKE**

The increased weights of the sections of the GIT, particularly the large intestine and the caecum, are in agreement with earlier reports in the literature (Stanogias and Pearce, 1985; Hansen *et al.*, 1992; Kyriazakis and Emmans, 1995; Pluske *et al.*, 1998). The digestion and processing of bulky foods requires the development of an appropriate gut microflora in the large intestine (e.g. Varel, 1987). The microbial fermentation of dietary fibre in the large intestine produces a significant amount of volatile fatty acids that provide between 0.05 and 0.28 of the pig's energy requirements (Stanogias and Pearce, 1985). Further, the rapid rate of passage of fibre through the stomach and the small intestine suggests that the role of these organs in fibre digestion is limited (Stanogias and Pearce, 1985). As important sites of fibre digestion, it seems sensible to assume that the large intestine and caecum will also, therefore, be important for the control of food intake on high bulk foods, however, a definitive role in the control of food intake has not been proven.

In Chapter 5 measurements on the GIT of pigs fed high bulk foods were made. This provided information about the way in which high bulk foods affected the GIT both within a treatment group and also across liveweights. It was found that, in general, the relative weight of the GIT tract was decreased with an increase in liveweight. If the size of the large intestine (LI) and the caecum are important for the control of intake on bulky foods, it might be expected that changes in absolute capacity for bulk with increasing liveweight would mirror changes in the absolute size of the LI and the caecum. When the two were compared it was found that the changes in capacity for bulk mirrored almost exactly the changes in the combined weight of the LI and caecum. The quadratic function

$$\text{Weight} = 0.0344.W - 0.000998W^2 \quad \text{kg} \quad (\text{rsd } 0.0794) \\ (\text{s.e. } 0.00245) \quad (\text{s.e. } 0.0000218)$$

where Weight, is the combined weight of the LI and the caecum and W, is liveweight, provided an accurate description of the relationship between the combined weight of the LI and caecum and liveweight. This function predicts that the combined relative weight of the LI and caecum ( $\text{g kg}^{-1} \text{ day}^{-1}$ ) will be 33.2 at 12kg, 30.8 at 36kg and 23.6 at 108kg. These are consistent with the changes in scaled capacity for bulk with an increase in liveweight.

The size of the GIT was measured in terms of weight, which is not a direct measure of capacity. An increase in weight does not necessarily mean that there will be an increase in capacity. An increase in weight will be brought about not only by an increase in size but also by an increase in gut wall thickness, the latter will not lead to an increase in capacity. However, the fact that changes in capacity for bulk closely mirror the changes in the combined size of the LI and caecum provides some evidence that the size of these organs may be closely linked to the capacity to consume food bulk.

### 7.3.3 MODELLING FOOD INTAKE DURING THE ADAPTATION PERIOD TO A NEW FOOD

In Chapter 6 a model was developed to predict food intake during the transition to equilibrium intake when there is a change in food to one of higher bulk content. The development of a model based on the assumption of maximum performance subject to constraints was justified in light of the evidence from Chapters 2 – 4. The importance of the adaptation period was emphasised in this Chapter and the assumptions made in the model represent an initial attempt at describing this phenomenon. The intention was that the model, rather than providing a definitive methodology from which to predict constrained food intake, would provide an insight into factors that are important for the control of food intake on bulky foods. Importantly areas where the model failed were highlighted.

The model failed to predict the initial food intake when there was a change to a food based on a highly indigestible material such as wheatbran and the intake of a non-limiting food where compensation occurred. The ability to deal with compensation in the model is difficult because a full understanding of the time course of compensatory growth is not currently available. More information about how long the compensatory response lasts, the rate at which it occurs and the extent to which it occurs is needed. In particular information about the way in which food type affects compensation is required.

The first failure of the model may be overcome by taking account of the time course of changes in digestive strategy following a change to a new food. Adaptation of the gut microflora is important for the digestion of all bulky foods. But for highly indigestible, non-limiting bulky foods, such as wheatbran, the initial reduction in food intake after a change in food may be more a function of the gut microfloras inability to efficiently digest the food rather than the bulk content of the food. As the bulk content, and hence the extent to which the food is limiting, increases it seems likely that the relative importance of a physical constraint will be increased. Hence, on bulky foods that are limiting, it would be expected the bulk content of the food

rather than digestive efficiency would determine intake. The initial reduction in food intake will be accurately predicted from knowledge of the maximum capacity for bulk and the bulk content (WHC) of that food. Therefore, the model should accurately predict the initial reduction in intake when there is a change to a food based on a digestible material such as sugar beet pulp, where the immediate problems of digestion are unlikely to be the same as those for a food based on, for example, wheatbran. The evidence is that it does.

Although able to accurately predict the initial reduction in intake, the model consistently underestimated the subsequent level of intake able to be achieved on a sugar beet pulp based food. This may be the result of the model underestimating the maximum capacity for food bulk. The model assumes that actual capacity will be increased by 0.01 units  $\text{kg}^{-1} \text{ day}^{-1}$  until a maximum capacity of 0.27 units  $\text{kg}^{-1} \text{ day}^{-1}$  is reached. However, this assumption did not lead to an accurate estimate of the intake achieved on a food high in sugar beet pulp. It was found that the accuracy of the model was significantly improved when it was assumed that there was no maximum capacity for bulk. The assumption of there being no maximum capacity for bulk cannot be seen to be general (see section 6.6.3) or even valid - ultimately there must be some limit to capacity. The inability of the model to predict the change in intake of a food based on sugar beet pulp highlights the fact that there is still a lack of understanding about how a bulk constraint to food intake operates and what the maximum capacity for bulk is.

## **7.4 THE MEASUREMENT OF WHC AND THE CAPACITY FOR FOOD BULK**

It was clear from Chapters 5 and 6 that there were specific problems with the methodology used to determine water-holding capacity (WHC). The scaled capacity for bulk (constant  $z$ ), units  $\text{kg}^{-1} \text{ day}^{-1}$ , varies with the methodology used to determine WHC. Higher values of  $z$  were obtained when methodologies that resulted in higher

estimates of WHC were used (Kyriazakis and Emmans, 1995, Tsaras *et al.*, 1998; Chapter 6). The constant  $z$  is multiplied by liveweight ( $W$ ) to give the maximum capacity for bulk at any given point in time. Constrained food intake (CFI) is then calculated as  $CFI = (z.W)/WHC$  ( $\text{kg day}^{-1}$ , Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998). Thus, CFI is dependent upon the value of  $z$ . Different values of  $z$  will lead to different predictions of food intake.

Throughout the course of this thesis WHC was estimated using the methodology of Tsaras *et al.* (1998), which was developed using foods based on sugar beet pulp, grass meal and soya hulls. However, in the current work there were problems with the sugar beet pulp foods not forming pellets at the bottom of the test tube after centrifugation (see section 3.3.1.2) and it is likely that this resulted in WHC being slightly overestimated. In Chapter 5 the methodology used to determine WHC was modified in an attempt to resolve this problem. It was found that centrifuging the samples to a constant weight improved pellet formation. Increasing centrifugation time in this way gave reduced, but more sensible estimates of WHC compared to the previous method. It is suggested that future WHC measurements should be based on this methodology.

For pigs of between 12 and 40kg values for the constant  $z$  of 0.17, 0.23 and 0.27 ( $\text{units kg}^{-1} \text{ day}^{-1}$ ) were suggested by Kyriazakis and Emmans (1995), Tsaras *et al.* (1995) and in Chapter 6 respectively. The difference between these estimates is not trivial and has large effects for the prediction of food intake, as a 26% increase in the estimate of  $z$  (0.17 to 0.23) could lead to a similar increase in the prediction of food intake. In each of the three cases mentioned above a slightly different methodology was used to estimate WHC. This led to progressively higher estimates of WHC for apparently similar foods. It seems that the differences in the methodology used to measure WHC may account for the increase in the value of  $z$ .

There are methodological problems with the measurement of WHC, which have a significant effect on the prediction of food intake and it is vital that these are resolved. There is clearly a need to standardise the methodology for WHC



determination if accurate food intake predictions and comparisons between the literature are to be made. It is difficult to make direct comparisons between the work of Kyriazakis and Emmans (1995), Tsaras *et al.* (1998) and Chapter 6. However, in light of the evidence presented in this thesis the value of  $z$  estimated by Kyriazakis and Emmans (1995) for pigs in the weight range of 12 – 40kg is considered to be low. The values of  $z$  estimated by Tsaras *et al.* (1998) and in Chapter 6 are considered to provide a more accurate estimate of the capacity for food bulk.

Estimates for the value of constant  $z$  have only been made in pigs of between 12 and 40kg. The work in Chapter 5 found that the scaled capacity for bulk (units  $\text{kg}^{-1} \text{ day}^{-1}$ ) declined with an increase in liveweight. The quadratic function

$$\text{Cap} = 0.230.W - 0.000476.W^2 \quad (\text{units day}^{-1})$$

was found to provide an accurate description of the relationship between absolute capacity for bulk (Cap) and liveweight (W). From this equation the scaled capacity for bulk (constant  $z$ ) at any given liveweight could be calculated as

$$z = 0.230 - 0.000476.W$$

In actual fact absolute capacity for bulk (bulk units  $\text{day}^{-1}$ ) is equal to the maximum capacity for bulk at any given point in time (i.e.  $z.W$ ) as absolute capacity for bulk is total daily food intake multiplied by the WHC of the food. Therefore, if it is possible to predict absolute capacity there is no need to estimate the value of constant  $z$  and CFI can be calculated as

$$\text{CFI} = (0.230W - 0.000476W^2)/\text{WHC}$$

The above equation provides an alternative methodology for predicting CFI without the use of constant  $z$ . However, absolute capacity for bulk and CFI are still dependent on WHC and so it is still necessary to standardise the methodology for WHC estimation.



## **7.5 PERFORMANCE ON HIGH BULK FOODS**

The predictions and hypotheses set down in Chapters 2 – 5 were based on the assumption that a bulky food was one that limited the energy and nutrient intakes, and hence the performance of the pigs to which it was fed. It was therefore, an important requirement that for all the experiments the bulky foods were indeed limiting. The use of wheatbran and sugar beet pulp as base materials for the bulky diets provided a comparison between two materials with different bulk properties. Wheatbran is a highly indigestible material with a relatively low 'bulk' content in terms of WHC, whereas sugar beet pulp is a highly digestible material with a high 'bulk' content as measured by WHC. The levels at which each of these materials was included in the diet was based on the results from previous work (Kyriazakis and Emmans, 1995; Tsaras *et al.*, 1998), and were fully expected to be limiting at the weight they were fed. Despite this throughout the experiments in this thesis pigs were able to perform significantly better, in terms of both food intake and gain, than had been expected.

On the basis of WHC alone it was not surprising that the foods based on wheatbran were not limiting even when fed to very young growing pigs. The bulk content of these foods as measured by WHC was not much higher than that of the control food. Pigs fed bulky foods based on wheatbran were therefore able to adapt to the food rapidly and to eat an amount that enabled performance to be maintained (Chapters 2 and 4).

However, the ability of young growing pigs to maintain performance on foods based on high levels of sugar beet pulp was not expected. It had been expected that over time, as liveweight increased, a food of a given bulk content would become less limiting (Chapter 4). However, it was surprising that foods based on 56%, 60% 70% and even 80% sugar beet pulp were not as limiting as had been expected even when fed over a limited weight range (Chapters 3, 4 and 5). The results here are not in agreement with work done in young, mature, individual and group housed pigs (Brouns *et al.*, 1991; Tsaras *et al.*, 1998; Vestergaard and Danielsen, 1998). The

reason for these differences is not clear, but as it stands, the evidence from this thesis suggests that the ability of growing pigs to cope with high levels of sugar beet pulp is much greater than previously thought and casts some doubt over the relative importance of a physical constraint to intake.

However, the apparently high level of gain achieved on the high bulk foods may, in part, be the result of an increased gut fill. Gut fill is significantly increased on foods with a high bulk content (e.g. Kyriazakis and Emmans, 1995; Chapter 5). The unexpectedly high level of performance achieved on the high bulk foods must, in part, be a reflection of this increased gut fill. In Chapter 5 some attempt was made to account for the effects for gut fill on liveweight gain. When the effects of gut fill were accounted for, gain on the bulky foods was substantially reduced (Chapter 5, section 5.5.2). Although the differences in gain between the bulky foods and the control food were still not significant, performance on the bulky foods was now much lower than that achieved on the control food at the same weight. It was also much more in line with that expected according to the results of previous work.

The effect of gut fill on the liveweight gain of pigs given foods high in bulk content may be large. There exists the need therefore, to account for the effects of gut fill when considering the performance of pigs on bulky foods. The inclusion of some estimate of gut fill in prediction models would allow more accurate estimates of liveweight gain. It seems likely that the gut fill equivalent of a food (that is, the gut fill resulting from the consumption of one gram of food) is a function of the bulk content of that food. It has been shown that, as the bulk content of the food increases so the does the gut fill equivalent, g gut fill/g food consumed, (Kyriazakis and Emmans, 1995; Chapter 5). In addition, the evidence from Chapter 5 is that the gut fill resulting from the consumption of a gram of food is constant across weights. If the gut fill equivalent of a food can be made a function of the bulk ingredient content of the food (i.e. percentage sugar beet pulp or wheatbran etc.) then it should be possible to predict the potential gut fill for a particular food. For example, using the data from Chapter 5 the relationship between gut fill and percentage sugar beet pulp (SBP) in the food was found to be linear and was estimated as

$$\text{Gut fill} = 0.7877 + 0.0233\text{SBP} \quad (\text{g g}^{-1})$$

The next step would be to calculate a rate of change in gut fill. To produce the equations for doing this is out with the bounds of thesis, but as was done in Chapter 5 it should be possible to calculate a rate of change in food intake between two points in time. The rate of change in gut fill would then be calculated as the rate of change in food intake multiplied by the gut fill equivalent of the food. The adjusted LWG (aLWG) is then estimated as LWG minus the rate of change in gut fill.

The results in Chapter 5 provide some evidence that the bulky foods fed during the course of this thesis were more limiting than the quoted results imply and suggest that the high level of performance able to be achieved on some of the foods was due to an increased gut fill. Although, the ability of pigs to cope with foods high in sugar beet were surprising, in most cases pigs fed the high bulk foods achieved a level of growth that was substantially less than that able to be achieved on the control food. Therefore, the intention that the bulky foods should limit the energy and nutrient intakes, and hence the performance of the pigs to which they were fed was, it is felt, achieved.

## **7.6 SUGGESTIONS FOR FUTURE RESEARCH**

Although there is still a lack of information about the way in which a bulk constraint to intake operates the idea that there is a physical constraint to intake is a useful one. Some ideas for future research have been suggested in the preceding sections. Of particular interest are the effects of feeding high bulk foods on meal patterns and the distribution of visits within those meals. As alluded to earlier the analysis of meal patterns may provide some information about where in the gastrointestinal tract the bulk constraint operates. In addition it will provide information about whether or not

the differences in STFB between foods seen at the level of visits are also obvious at the level of meals.

This thesis has highlighted the importance of the adaptation period when considering food intake on high bulk foods and yet this period is mostly ignored when it comes to reporting and predicting food intake. It is apparent that currently there is a lack of information about the adaptation period to high bulk foods. Adaptation is thought to involve the adaptation of the gastrointestinal tract to the increased gut fill and digestion of high bulk foods, but further research into this area is required, particularly about the rate and length of adaptation; does it differ between foods, breeds and degree of maturity? Some attempt was made to look at the effect of degree of maturity on adaptation in Chapter 5. The results suggested that adaptation took longer in pigs fed SBP<sub>80</sub> at 108kg. It is not clear whether the increased adaptation time was the result of the increased bulk content of the food or increased liveweight. Degree of maturity was confounded with the type of food fed (a more bulky food was fed at 108kg, than at 12 or 36kg). Previous nutritional history is known to affect adaptation and quantification of the effects of previous nutritional history on adaptation would aid prediction methods. In addition as discussed in section 7.5, the development of predictive equations for estimating gut fill would allow improved predictions of liveweight gain on high bulk foods.

Serial slaughter experiments would provide further information about the way in which the GIT adapts to high bulk foods and the rate at which adaptation occurs. If the adaptation of food intake over time could be shown to mirror the adaptation of the GIT over time this would provide strong evidence that the capacity of the GIT tract was important for the control of food intake on high bulk foods. If WHC were an appropriate measure of bulk content, measurements of WHC on the gastrointestinal contents would provide information about the way in which WHC changed with passage through the gut and perhaps give an indication of where the bulk constraint operates. Serial slaughter experiments could also be used to provide information about the way in which the GIT microflora adapt to high bulk foods. A series of samples from the GIT could be cultured to provide information about the

way in which the gut microflora developed in response to high bulk foods and the rate at which adaptation occurred.

A physical/digestive constraint to food intake is evident particularly in the initial stages after a change to a food of high bulk content. It would be interesting therefore to try and ascertain where in the gastrointestinal tract that constraint to intake operates. Analysis of meal patterns may provide some evidence as to whether or not the constraint operates at the level of the stomach, but it seems more likely that the large intestine will be important for the control of food intake on high bulk foods. The large intestine is an important site of fibre digestion and it is this area of the GIT that is most affected, in terms of size, by the feeding of high bulk foods. As an important site of microbial digestion the role of the large intestine in the control of food intake on high bulk foods could be tested by reducing fermentation in the hindgut. If the large intestine plays an important role in the control of food intake on bulky foods, it would be expected that a reduction in hind gut fermentation would have no effect on the intake of a low bulk control food, but that a significant reduction in the intake of a high bulk food would occur. Fermentation in the large intestine could be reduced through the addition of antibiotics to the food. To completely remove fermentation in this way would be difficult. Most of the common antibiotics have limited efficacy against the major fermenting organisms in the gut (*Bacteriodes*, *Lactobacilli*, *Fusobacterium* and *Eubacterium*). Use of one of the few remaining antibiotic growth promoters would also be unlikely to have the desired effect. However, a beta-lactam/beta-lactamase combination was found to be effective in reducing bacterial fermentation in the short term (Betriu *et al.*, 1999) and a mixture of Clamoxyl powder (80g/kg day), Neobiotic powder (32g/kg day) and Zinc bacitracin (800g/kg day) was also found to significantly suppressed fermentation (Edwards *et al.*, 1989). A preferable, but expensive, alternative to the use of antibiotics would be the use of germ-free animals. These animals would be born and maintained in a germ free environment and would be expected to be free from microbial 'contamination', so that fermentative micro-organisms would not be present in the hindgut.

## **7.7 GENERAL CONCLUSIONS**

Currently there is a lack of information about the control of food intake on high bulk foods. The aim of this thesis was to try and provide a further insight in to the factors that are important for the control and prediction of food intake on bulky foods. The first part of the thesis aimed to distinguish between the two current frameworks available for the control and prediction of food intake on high bulk foods. The idea that animals aim to maximise oxygen efficiency is rejected. It is clear from the work in this thesis that this framework is not appropriate for use in pigs, as it cannot account for the observed variation in food intake on high bulk foods.

The work in this thesis provided no reason to reject the assumption that animals aim to maximise performance subject to one of several limiting constraints not being exceeded. A model based on this assumption was able to predict food intake with a reasonable degree of accuracy, suggesting that the underlying theoretical assumptions are sensible. Therefore, it is concluded that this framework can be used as a basis for accurate food intake prediction.

A relationship between degree of maturity and capacity for bulk has been established. It was shown in Chapter 5, that relative capacity for bulk decreases with an increase in liveweight and an equation for predicting capacity for bulk was developed. Moreover, it was shown that the increase in capacity for bulk mirrored the increase in the size of the LI and the caecum, suggesting that the size of these organs may be linked to the capacity for food bulk. The model in Chapter 6 developed a methodology for predicting food intake during the adaptation period to a new food. The period of adaptation is generally ignored when it comes to predicting food intake. However, the extent to which a food is limiting (i.e. physically constrained) depends on the weight of the pig, previous nutritional history and the length of time for which the food has been given. The idea that changes in equilibrium intake over time are the only relevant changes in food intake does not seem sensible in the light of the evidence in this thesis. It may be more relevant, therefore, to develop a predictive methodology that predicts the changes in

constrained food intake both during adaptation and beyond, rather than just predicting changes in adapted food intake over time. The beginnings of a methodology for doing this are now in place. However, it was apparent from the work in Chapter 6 that it is still not clear what the maximum capacity for bulk is. Capacity for bulk on a food high in sugar beet pulp was greater than expected, and an attempt to estimate capacity from the bulk content of the food led to capacity during adaptation being underestimated. The reasons for this are unclear, it seems that capacity for bulk, at least on sugar beet pulp, is much greater than is assumed in the model. This highlights the fact that there may be other factors not considered in the model that are important for the control of intake on high bulk foods. More information about the way in which the GIT and digestive strategies develop during adaptation may help to improve the understanding of the adaptive process and how it differs between foods, ultimately this will allow the improved prediction of constrained food intake.

This thesis has been successful in achieving its objective of improving the prediction of the voluntary food intake of growing pigs on poor quality foods. It has shown that the idea of maximum performance subject to constraints is an appropriate framework for the control and prediction of food intake on high bulk foods. A relationship between liveweight and capacity for bulk has been established and a methodology for predicting changes in constrained food intake during the adaptation period to a new food has been developed.

***“It has all been very interesting”***

Lady Mary Wortley Montagu, last words, 1762

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